

JOURNAL OF
THE ROYAL SOCIETY
OF
WESTERN AUSTRALIA

VOLUME 60 (1977-78)

The Royal Society of Western Australia, Inc.

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Annual Report of Council for the year ending 30 June 1977

Membership

Membership of the Society stands at 246 Ordinary and Associate members, 15 Honorary and 1 Student member; a total of 262.

During the year there were 5 resignations and 3 deaths—including those of Mr. A. C. Shedley and Professor D. A. Herbert, both Honorary members and the latter a Foundation member of the Royal Society of Western Australia. Thirteen Ordinary members were admitted during the year and at the 1976 Annual General Meeting Emeritus Professor R. T. Prider and Mr. R. D. Royce were elected to Honorary membership.

Council

Eleven meetings of Council were held during the year. Attendances were:

Dr. P. R. Wycherley	10
Dr. B. E. Balme	6
Mr. P. R. Atkinson	8

Dr. A. E. Cockbain	9
Mr. S. J. Curry	10
Mr. C. E. Dortch	7
Dr. B. B. Lamont	5
Dr. J. K. Marshall	8
Mrs. A. Neumann	5
Mr. L. J. Peet	4
Mrs. G. Perry	9
Mr. M. W. Perry	8
Dr. P. E. Playford	6
Dr. J. C. Taylor	9
Mr. C. F. H. Jenkins	5
Assoc. Prof. A. J. McComb	3

Mr. C. F. H. Jenkins was co-opted onto Council during the year and filled the vacant position of Vice-President. Assoc. Professor A. J. McComb returned after leave of absence during 1976-77.

Meetings

The Annual General Meeting was held on 19 July 1976 in Mineral House when Dr. B. E. Balme delivered the Presidential address entitled "The succession of Western Australian fossil floras".

Dr. P. R. Wycherley the incoming President was then installed by the Chief Justice of Western Australia. The Honourable Sir Lawrence Jackson K.C.M.G.

Ordinary meetings were held in September, October, November, December and June. Speakers and topics were:

September: Professor P. F. Harris "Tristan da Cunha—a volcanic island".

October: Professor S. Cobb "Evolution of social systems in Lobsters".

November: Dr. B. F. Phillips "Recent research on the larvae of the Western Rock Lobsters".

December: Film—"The making of a Natural History film" and exhibits.

June: Mr. J. N. Green—"The excavation of the V.O.C. ship Batavia".

The Jarrah Forest Symposium

On three consecutive Monday evenings in March and April a series of nine lectures were given on the Jarrah Forest. The lectures, held in conjunction with the University of W.A. Extension Service, covered the physical geography, biology and human use of the forest. The Symposium was well attended by both members and the general public.

The speakers were Dr. S. Wilde, Mr. A. M. Scott, Mrs. S. Hallam, Dr. N. Marchant, Dr. S. Davies, Dr. J. Marshall, Dr. A. J. Peck, Mr. G. White and Dr. E. Hopkins. The session chairmen were Dr. D. Merrilees, Professor A. R. Main and Dr. M. J. Mulcahy.

Library

Five new exchanges were entered into during the year bringing the total to 255. The Library's emphasis continues to be on publications otherwise unavailable in Western Australia, and it continues to receive wide use through the inter-library loan system. \$400 was expended on the binding of accumulated serials.

Journal

Parts 1-3 of Volume 59 were issued during the year and part 4 will be published shortly. Volume 59 will contain papers covering most facets of the Society's activities.

General

Ian Clunies Ross Memorial Foundation

During the year the Society became accredited to the Ian Clunies Ross Memorial Foundation. The Foundation is an independent body whose object is to promote and further the development of scientific research; specifically by providing facilities for a National Science Centre. The centre—Clunies Ross House—is located in Melbourne and provides facilities for many scientific societies. The Foundation recently opened a "Science Centre" in Western Australia with the aim of eventually providing comprehensive facilities for local scientific groups. Council decided that the Royal Society should play an active role in these developments.

Royal Society Journal—150th Anniversary Volume

Planning is well advanced towards the production of an anniversary volume for the State's sesquicentennial year. It is planned to include both historical and contemporary aspects of the natural and social sciences in Western Australia.

Acknowledgements

The Society thanks the State Treasury and the Government Printer for co-operation in publishing the Journal. It is also indebted to the W.A. Museum for housing the library. The Minister for Mines has kindly allowed the Society to hold its General Meetings at Mineral House.

P. R. WYCHERLEY,
President.

M. W. PERRY,
Joint Hon. Secretary.

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Regeneration after fire in King's Park, Perth, Western Australia

by A. M. Baird

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Manuscript received 22 April 1975; accepted 13 December 1976

Abstract

Fires, both devastating wildfires and controlled burns, have been frequent in King's Park over the past thirty years, and some changes in the vegetation over this period have been recorded. A major one has been the spread of the South African veld grass *Ehrharta calycina*, aided by fires and firebreaks. The native bush is fire adapted; none of the tree species and few of the shrubs are killed by fire. The undergrowth is rapidly built up again after a fire since most shrubs sprout vigorously from lignotubers or deep tap-root systems and monocotyledons make rapid recovery from undamaged underground apices. The few species killed by fire, with two exceptions, regenerate freely from seed. Nevertheless, too frequent fires have tended to reduce or eliminate certain species.

The regeneration in the first year differs with the season of the burn, spring burns favouring shrubs and autumn burns favouring the herbaceous species. Details are given for the progress of fire succession after particular burns at different seasons, and of the response to fire of some of the more important species.

It is concluded that in unmodified bush, control burning of small areas could be used effectively to maintain healthy undergrowth and a pleasing diversity. The problem of control of vegetation has been immensely complicated by the presence of veld grass and other weed species so much more aggressive than their native counterparts and apparently favoured by any programme of burning.

Introduction

Fires in eucalypt forests are of such vital importance that there is an extensive literature, most of it understandably concerned with forest trees and to a lesser extent major understorey species. The observations recorded in this paper have, as far as possible, included all species of the undergrowth, the vulnerability, type of regeneration and rate of recovery after fires at different seasons.

The area concerned is in King's Park, Perth, Western Australia, a reserve in which about 250 hectares is uncleared bush. An account of the park with a general description of the flora and fauna was given by Main and Serventy (1957). A more recent paper (Beard 1967) discussed the eucalypt woodlands comparing their present condition with the presumed original state.

The vegetation is a *Eucalyptus-Banksia-Casuarina* woodland with a dense low (30-100 cm) understorey of sclerophyllous shrubs and harsh monocotyledons (Fig. 1). It varies from an almost pure *Banksia-Casuarina* woodland through stands with Jarrah (*Eucalyptus marginata*) or Jarrah and Marri (*E. calophylla*) as an overstorey to the *Banksia-Casuarina*, to a more open woodland with tall Tuart (*E. gomphocephala*).

Notes and photographs of the regeneration and some measurements of rates of growth following different fires have been made over many years. Some permanent quadrats laid down in 1936-40 have been remapped at intervals for more than 30 years. Observations have been mainly in the south-west half of the park and adjacent University land.

In a climate with a cool wet winter and long hot dry summer the fire hazard is very high, due both to the climate and the highly inflammable vegetation. Fires in the park have been frequent and have occurred in all seasons. They fall mainly into 2 groups: devastating wildfires in mid-summer (January-February), and mild burns covering smaller areas in spring and autumn.

The most extreme fires burn the foliage and may kill the upper branches of the trees; less intense ones do not burn but scorch and kill the leaves which fall later (Fig. 2A); the ideal control burn leaves the canopy even of the small trees unharmed (Figs. 2B and 11A). In all fires except those over recently burned sections the shrub layer is burnt off to ground level, except for a few dead sticks of some of the stronger shrubs. In severe burns the ground surface is left as white sand with patches of ash and charcoal (Figs. 2-3). In a mild burn only the loose litter is burnt, leaving the older organic layer.



A



B



C

Course of regeneration during the first year

Regenerations after fires of December 1950, January 1958 and January 1973 in the same area and January 1970 in a different site are described as typical of mid-summer fires. However, it must be remembered that no two fires are exactly the same, nor are the following weather conditions. Damage to trees was severe in all these fires, most extreme in 1973. The state of the trees and the ground surface immediately after, or within a few weeks of the burn, are shown in Figures 3A-D.

Growth

The first plants to grow are the *Xanthorrhoeas* (Blackboys) (Fig. 3). The burnt off leaves continue basal growth and new leaves appear from the well protected apex. Sedges, particularly *Tetrarhizis*, grow almost as soon from underground basal extension of the burnt off leaves. New leaves of the cycad *Macrozamia* appear within a few weeks, grow extremely rapidly and reach full length in about 4 months (Fig. 3D).

Some of the deep-rooted shrubs sprout within 2-3 weeks of being burnt, e.g. *Persoonia*, *Jacksonia*, *Daviesia* (4 species), *Leucopogon*, *Stirlingia*, *Scaevola*, *Petrophile* and *Hardenbergia* (a climber) and some others, e.g. *Hibbertia*, *Oxylobium*, less vigorously. All these show as isolated tufts in the extensive areas of bare ground (Figs. 3 and 4). Figures 3A, B, C, D, all show the regeneration before the winter rains. The soil is exposed to the full heat of the summer sun to be followed by the battering and leaching of the heavy winter rain.

Shortly after the commencement of the effective winter rains there is a sudden flush of growth of herbaceous plants. First are the geophytes, *Burchardia umbellata*, *Sowerbaea*, *Cacasia*, *Eryngium*, *Drosera* spp. and orchids. Annual weeds germinate quickly and are very conspicuous at this stage in disturbed areas, being more vigorous than the native annuals, which also germinate, but more slowly. Of these, *Calandrinia corrigioloides* and, to a lesser extent *C. liniflora*, are very abundant although rarely seen in unburnt areas.

The winter rain also increases the growth of the shrubs. New growth appears on plants which had started before rain. In many cases, particularly *Scaevola* and *Kennedia*, this winter growth has much larger leaves than those produced in the summer. New clusters of shoots appear above ground on plants which had made little or no growth before the rain. Those species which normally grow mainly in winter, e.g. *Phyllanthus*, *Hybanthus*, now grow rapidly, while others grow slowly until the spring warmth. Seedlings of trees and shrubs also appear soon after the rains. At this stage the 'patchiness' of the ground cover is very noticeable. Many species are very unevenly distributed, and the total shrub cover varies greatly from place to place.

Flowering

The flowering of herbaceous species follows the same progressive seasonal pattern after fire as in unburnt bush, e.g. *Drosera erythrorrhiza* in May, other species later; *Lomandra preissii* very soon after rain followed by *L. micrantha* and *L. endlicherana*. Orchids come into flower from May to November, each species having a short flowering period. *Caladenia flava*, one of the commonest, is illustrated (Fig. 4A). The greatest show of herbs is in spring and early summer, with *Burchardia*, the most widespread and abundant species (Fig. 5B) and other liliaceous species. Annuals on the average flower later than the geophytes but again there is a sequence of flowering, e.g. in the composites the order is *Podolepis*, *Podotheca* (Fig. 4C) and *Waitzia*.

By far the most conspicuous species in October-November, is the annual grass *Stipa compressa* with its long golden awns (Fig. 4D). It dominates the burnt areas, obscuring the lower shrub regrowth. The tall white flowering spikes of *Xanthorrhoea* project above this sea of grass and the dark brown inflorescences of the two species of *Haemodorum* show up against the pale grass (Fig. 3F). Both *Xanthorrhoea* and *Haemodorum* flower profusely after fire but very rarely in unburnt bush.

Most of the common shrubs, e.g. *Daviesia*, *Hibbertia*, *Oxylobium*, *Hovea*, *Hypocalymma*, *Leucopogon* and *Stirlingia*, do not usually flower in the first season after a late or mid-summer burn. None were seen in flower in the sites burnt in 1973. However, some early-blooming species do flower in the first year—notably *Scacvola canescens* which flowers from May onwards, even on 5-7 cm of regrowth. In early spring the creepers *Hardenbergia* and *Kennedia*, and some of the small herbaceous perennials, e.g. *Hybanthus* and *Monotaxis*, are in flower.

In general, flowering for sprouting shrubs is particularly good in the second and third years after fire. In September to October 1974, flowering was spectacular in the less weedy parts of a January 1973 burn, after two above-average rainfall winters and a virtual absence of tree canopy. Kangaroo paws have many times been noted as particularly abundant in the third and fourth years when new seedlings from the fire are flowering. The surviving old plants bloom in their first season of regrowth.

In the Tuart areas the course of the regeneration is similar to that described above for Jarrah-Banksia communities, although there are some different species (see species list) and in general a more herbaceous undergrowth. The common *Daviesia* spp. are almost absent. *Macrozamia* is far more common. Of the species almost confined to the Tuart, *Clematis*, *Rhagodia*, *Scaevola holosericea* and the thoroughly naturalised South African *Pelargonium capitatum* all

Figure 1.—Types of vegetation. A.—Typical Banksia-Casuarina woodland with dense low shrub undergrowth; *Acacia pulchella* in flower; August 1960. B.—Tuart with *Grevillea vestita* in flower. C.—Tuart with veld grass; *Dryandra* in right hand corner.



make good regrowth. The tall shrubs *Conospermum triplinervium*, *Dryandra sessilis* and *Grevillea crithmifolia* are killed by fire whereas *Grevillea vestita* suckers freely from horizontal roots.

The fireweed distinctive of the Tuart association is the tall, semi-herbaceous *Anthocercis littorea* (Solanaceae). It is killed but seedlings are numerous and grow rapidly, reaching 1-2 m and flowering within a year of the fire.

Where a fallen tree trunk has burnt to ash a small orange discomycete fungus appears in the first year followed by *Funaria hygrometrica* fruiting in the second year. Exuberant growth of *Funaria* on burnt ground is a well-known phenomenon in many moist climates, but it is interesting that it also occurs in this habitat not particularly favourable to mosses.

Season of burn

Early regrowth after fires differs markedly with the season of burns; in general spring burns favour shrubs and autumn burns favour herbaceous plants.

Burns in March 1952 (Fig. 5), and March 1956 and 1957, will serve as examples of autumn burns in Jarrah woodlands. As with any fire, blackboys and sedges were the first to grow, little else appearing before the first rains, which were followed by a flush of herbaceous shoots. There was also some sprouting of shrubs through May and June. These shoots mostly remained short until the warmer weather in spring, and did not flower until the following year. An exception was the winter growing *Phyllanthus*, which grew rapidly and reached flowering in August of the first year. Through winter the herbaceous geophytes, *Burchardia*, *Arthropodium*, *Caesia*, *Sowerbaea*, with the sedges and the smaller annuals, formed the bulk of the ground cover with the short shrub shoots more or less obscured. Figures 5A, B and C show the same site burnt in March 1952—A. 2 days after the fire, B. *Burchardia* in flower in September, and C. *Stipa* in flower in October. *Podotrochea* (Fig. 4C) and other smaller annuals were also abundant. Equally spectacular displays of *Burchardia* and of annuals later, occurred after fires in other areas in March 1957.

Spring to early summer fires result in rapid and vigorous shrub growth which, with equally rapid growth of blackboys and other fibrous monocotyledons, goes far to restore the undergrowth before the late summer drought. The effects of several control burns in early November have been watched and measurements recorded of average rates of growth of several of the common sprouting species. In all sites regrowth was very good, shoots of shrubs showing within 3-6 weeks of the fire, growing rapidly and continuing later into the summer than is normal for unburnt plants. Shrub regrowth was advanced enough for flowering in following

winter to spring of *Daviesia* spp., *Hibbertia* spp., *Oxylobium*, *Stirlingia* and others which do not flower until the second season after an autumn burn. Figure 5E shows the same site as Figure 5B and at the same time of year but after another fire in early summer. Figure 2B shows regrowth of shrubs in June after a November burn and also illustrates the trees with even low branches undamaged and tall shrubs (*Jacksonia*) unburnt. This was an ideal control burn although the fire hazard had been high; minimum damage was done and only the loose surface litter was consumed. This may be compared with conditions after the wildfire of 1973 (Fig. 3). Figure 11A shows regrowth after another mild early summer fire.

A spring burn followed by enough rain to germinate seeds may result in seedling death over summer as there is not time enough for the tap root to penetrate deeply before the dry season. An example of this was recorded in 1949 where of numerous seedlings of *Acacia pulchella*, which grew after an October fire, not one survived the summer. In an adjacent quadrat burnt in January seeds did not germinate until May and after growing through the winter and spring were safely established before summer. The increase of the *Acacia* here was from 3 plants before to 69 after the fire. For annuals a fire before the plants have set seed reduces the seed available for next season. Winter and early spring fires damage geophytes when foliage is burnt off after the new growth has depleted storage organs. One June burn resulted in very poor flowering of *Burchardia* compared to adjacent unburnt bush, and in marked contrast to the rich flowering after autumn burns.

It must be emphasised that although autumn burns undoubtedly favour herbaceous plants they are not necessarily unfavourable to shrubs. In fact, in the absence of competition from veld grass, the slower early leafy growth and delayed flowering may eventually result in a sturdier plant.

Continuing regrowth

For the first 2 or 3 years after a fire shrubs are erect and vigorous with a variable amount of bare ground between them. As lateral branching increases the plants spread and become straggly; the shrubs overlap each other and the associated spreading fibrous monocotyledons.

The general vegetation level is restored early and changes very little, but the density of cover increases as branches multiply and new shoots grow from ground level. Certainly tall shrub species regenerating from seed in the lower layers eventually grow tall and project above the general level, but as these shrubs tend to occur in thickets in restricted localities they do not invalidate the picture of a predominantly uniform low level of undergrowth.

Figure 2.—A.—Photo taken the day following a fire in February 1959. The fire did not go through the canopy but the leaves were scorched and fell later. The old tree in the centre was burnt through and was still smouldering, fresh white ash in foreground. This is part of the stand referred to in Table 1. B.—A mild control burn; even tall shrubs and lower branches of trees not burnt. Photo May 1953 six months after the fire in November 1952. Shrub regrowth well established.

Samples of bush at different intervals after fires are shown in Figures 6A-F.

With age the percentage of dead wood increases, and leaf and twig litter from trees accumulates and tends to cover the shrubs. After about 10 years, or sometimes less, *Daviesia* spp. in particular and also *Petrophile linearis* and *Conostephium pendulum* show definite signs of deterioration, and become infected with scale insects and sooty mould. *Stirlingia*, so strikingly vigorous in its growth and flowering after fire, becomes an inconspicuous component, non-flowering and with stem increments and leaf size steadily diminishing so that old plants have small tufts of leaves on long stems which tend to become prostrate. *Hibbertia* and *Oxylobium*, on the other hand, continue to grow and flower, although in somewhat tangled mats. *Acacia pulchella*, with its single main stem, continues to grow well and flower profusely for 8-10 years, but over subsequent years many plants begin to die. The smaller *Gompholobium* suffers a similar fate.

In stands not burnt for 20 years or more, there is a real suppression of the undergrowth and a heavy build-up of leaf and twig litter (Fig. 6D). Nevertheless, few plants are killed and some grow with only the tips of long trailing stems showing through the deep litter. The quite small plant, *Monotaxis*, is one of these. *Hibbertia*, *Hovea*, *Pimelea*, *Conostephium* and others continue to grow and flower unless totally smothered by *Casuarina* litter. The greenhood orchids, particularly the tall handsome *Pterostylis recurva*, are always at their best in long unburnt areas with deep organic matter. One small area which had escaped fire for at least 60 years and in which several fire-sensitive species were persisting has, unfortunately, been absorbed into a developed area.

Long term effects of repeated fires

These include progressive damage to trees, soil deterioration, reduction or elimination of weakly regenerating species and increase in weed species. Benefits of periodic burning include removal of senile and diseased branches, destruction of insect and fungus pests, rejuvenation of sprouting shrubs many of which seem to require periodic burning for healthy growth and flowering, and production of new crops of some short-lived shrubs which need fires for renewal from seed. The balance between good and bad effects depends on the extent, severity and frequency of fires, and because of the differing responses of different species there is no absolute optimum.

The greater damage by severe and extensive wildfires than by small mild burns needs no re-statement. Irreparable damage to trees where

fire has eaten into the heartwood or killed main branches is obviously more likely in wildfires, as is destruction of organic matter in the soil. In the park most of the common species survive the wildfires and make vigorous growth and flower profusely after mild or severe burns. The undergrowth may, in fact, benefit initially from the reduced transpiration and greater light where the tree canopy has been destroyed, but in the long term, with repeated fires, loss of organic matter and excessive leaching of the soil probably has a deleterious effect, particularly on the smaller species. Sampling in many sites has shown, as would be expected, a clear relationship between organic content of the sandy soil and its water holding capacity which, in the absence of organic matter (there is no true humus), is extremely low.

Fires every year, or as often as the bush will carry fire, are very detrimental to the undergrowth. This was seen in University land where deterioration was evident even before the veld grass overran the area. Regrowth of the sprouting shrubs became weaker with each succeeding fire and a number of the less vigorously regenerating shrubs died out, e.g. *Hovea* and *Pimelea* and *Phyllanthus*. The fire-sensitive species, *Acacia pulchella* and *Gompholobium tomentosum*, were eliminated. Deterioration of the soil was suggested by the abnormally small size of many annuals and herbaceous geophytes. This was very noticeable in *Drosera* species, in *Trachymene pilosa*, and in small annual grasses and composites. An orchid, *Lyperanthus nigricans*, recognised as one which flowers well after bush fires, had completely ceased to flower, although small leaves appeared annually for many years.

Response to fire of plants in relation to their life form

In an attempt to include most of the 230 species and make some generalizations—always dangerous as every species behaves differently—species are grouped and discussed under life forms.

Trees

None of the tree species is fire-sensitive, all are capable of sprouting from epicormic buds although some suffer more damage than others. A detailed survey after a severe fire in a dense *Banksia-Casuarina* stand showed that in this particular fire crowns of a few of the larger trees remained more or less undamaged but most mature trees had the leaves killed by heat although the fire did not run through the canopy (Fig. 2A). These sprouted up the upper branches, as in Figure 7E. Smaller trees had the upper branches killed and sprouted from epi-

Figure 3.—These photographs all show regrowth after a fire on 16 January, 1973. A.—Soon after the fire. B, C, D April 1973, three months after the fire. B.—*Xanthorrhoea* tufts, fallen leaves, bare sand. C.—Regrowth of *Daviesia divaricata* (centre and others with burnt old stems). *Stirlingia* (right), *Schoenus grandiflora* in front of bent stem. D.—*Macrozamia* and *Persoonia* regrowth. E.—Same site as A one year later, April 1974. Many Eucalypt coppice shoots, shrub regrowth partially obscured by dry grass (*Daviesia nudiflora* in front of bent tree trunk). F.—*Xanthorrhoea*, *Stipa compressa* and *Haemodorum* (2 spp.); November 1973; approximately the same site as B. G.—Epicormic shoots starting on some burnt trees; *Xanthorrhoea* with blackened trunks; June. H.—Same site as G one year later; poor recovery of trees; veld grass on edge of firebreak.



cormics up the trunk as in Figure 5, while saplings under 2 m were mostly killed to ground level and produced coppice shoots. Many of the smallest saplings were completely killed. Actual figures recorded in part of this survey are given in Table 1. This is probably a common pattern in summer fires—and it has been noted in

several others also. Damage was more severe in the January 1973 fire, examples of which are shown in Figures 3, 7 and 11.

Casuarina fraseriana is very badly damaged; the bark is thin and rough and easily burnt. Most trees of this species in the park have parts of the trunk dead and hollowed out by repeated

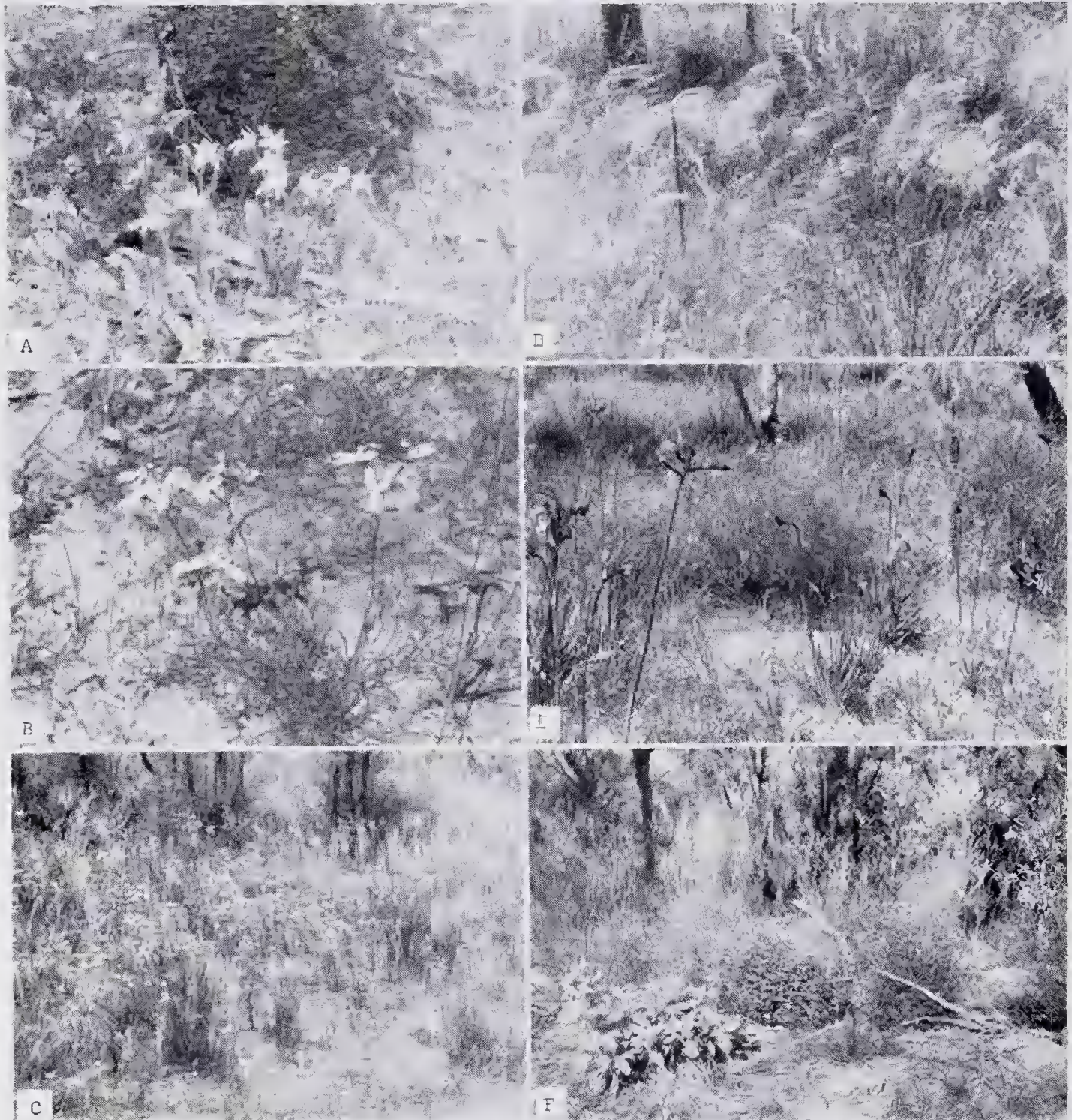


Figure 4.—A—D Herbaceous species in the first season after fire. A.—*Caladenia flava*. September 1958, after January fire. Note the hard undamaged bark of *Banksia menziesii* (leaves on ground). B.—*Stylidium schoenoides*. Note different positions of the column ("trigger"). September 1970 after a January fire. C.—*Podotheca chrysantha* and *Stipa*. October 1955, after a May fire. D.—*Stipa compressa* with long awns and sparse *Ehrharta* with taller panicles. October 1961 after a December fire. E.—Regrowth in second year. *Anigozanthos manglesii* (Kangaroo paw) in flower and bud in foreground, *Daviesia juncea* (centre) and other shrubs, August 1974, after January 1973 fire. F.—Regrowth of various shrubs. Left to right: *Daviesia divaricata*, *Helichrysum cordatum*, *Stirlingia* (behind with tall inflorescences), *Oxylobium* (centre), *Leucopogon propinquus*; Monocotyledons in foreground. June 1974, after a November 1973 fire.

fires, and poor incomplete canopies. The trees, however, cling to life very persistently and will survive with only strips of living tissue up the trunk. This capacity to survive in a mutilated condition has undesirable consequences. The mass of shoots up the burnt trunks persists for

very many years as there is no healthy crown to shade out lower branches and eliminate weak saplings, as would normally occur in over-crowded stands. Hence flowering undergrowth species and healthy seedling trees are suppressed and the mass of branches from the ground up

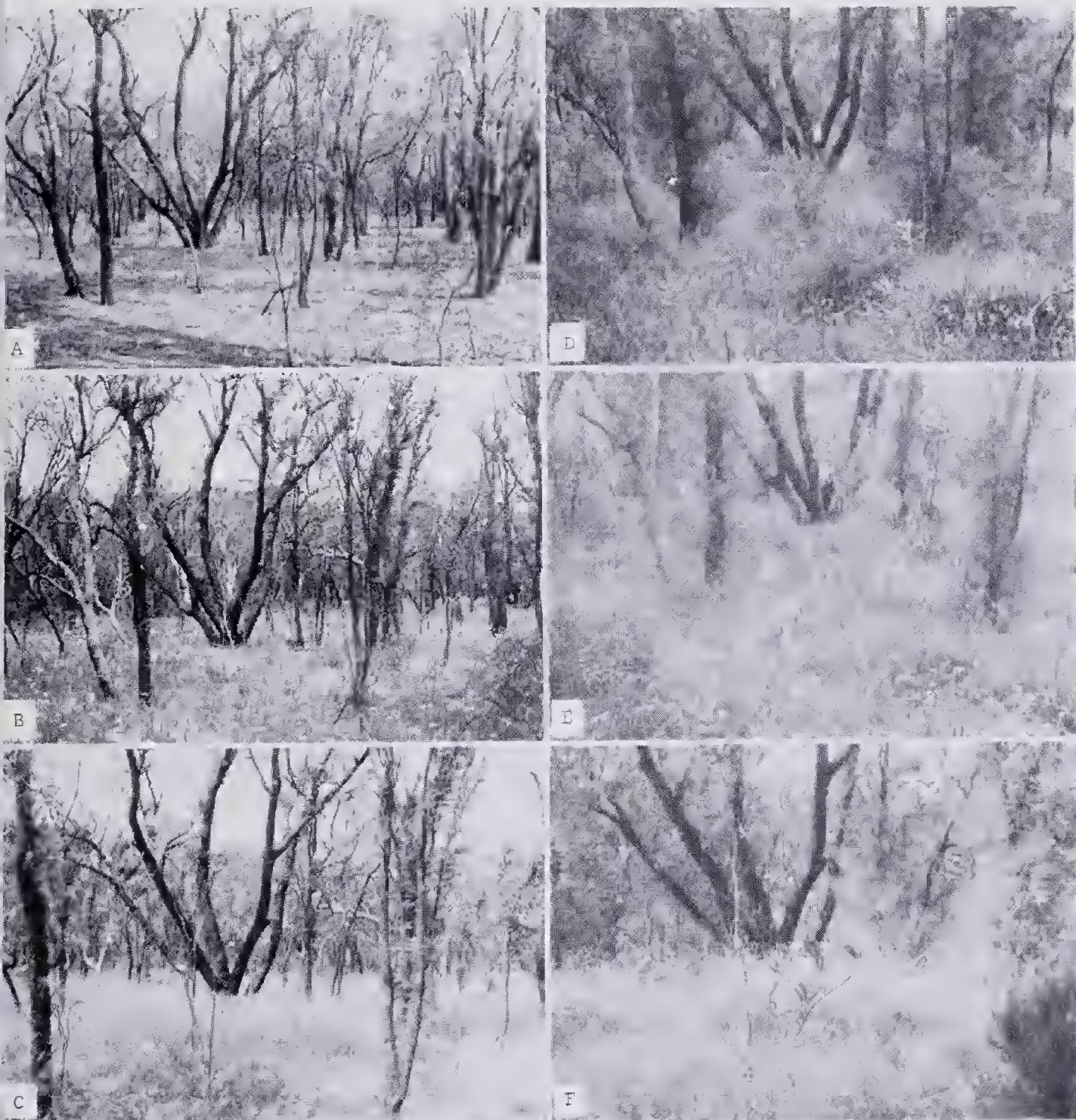


Figure 5.—Series taken to the same tree following a severe fire in March 1952. A.—March, 2 days after the fire. The section in the background was not burnt. B.—September, *Burchardia* in flower. C.—October—*Stipa compressa* in flower dominating the ground cover. D.—A year later than C, November 1953. Note epicormic shoots on *Casuarina* trunks, a *Banksia* seedling plant just left of forked *Casuarina*, dead *Acacia pulchella* (non-sprouting) extreme right corner, *Briza maxima* against shadow left of this and absence of *Stipa compressa*. E.—September 1955, after a second fire in November 1954. Compare with (B) September 1952. *Burchardia* in flower as (B) but shrub regrowth much greater, *Hibbertia* in flower in foreground. The seedling *Banksia* in (D) has been killed but the coppice shoots of *Banksia* sapling centre have grown taller. F.—October 1959, Veld grass now well established.

creates a dangerous fire hazard.

Seedlings of *Casuarina* are found but their occurrence seems very irregular and probably depends on the right combination of ripe seed released, but not burnt, and suitable conditions for germination. After the March 1952 fire (illustrated) carpets of seedlings were found under several old female trees. The seedlings were first seen in early June when slender shoots

were just appearing between the small cotyledons. By mid-August the still unbranched shoots averaged 7-8 cm in height, and in late September were about 10-15 cm with some branching. Two months later their height was mostly 16-20 cm with considerable increase in the growth of their branches. By December their growth had apparently ceased and some plants had yellowed. Over the summer a few plants



Figure 6.—Examples of continuing regeneration. A.—Two years after fire in December 1950; shrub layer re-established, tree canopy partially restored. (*Casuarina* right, *Banksia* left.) Shrub cover mainly *Danisia* spp., *Oxylobium*, *Xanthorrhoea* with many smaller plants not recognisable in the photo. B.—*Acacia pulchella* in flower, September 1953. Growth from seed after December 1950 fire. C.—Same stand in the seventh year after fire; *Acacia pulchella* now well above general level, left and centre back. *Jacksonia furcellata* and *Banksia menziesii* both also grown from seed after the 1950 fire. D.—Unburnt site under *Casuarina*, accumulated needles suppressing undergrowth. E.—*Hibbertia* in flower in the second year after the January 1973 fire. F.—Unburnt for probably 12 years, at least 10 years. *Hibbertia* in flower in a tangle of bushes. *Macrozamia* leaves on left.

Table 1

Part of an assessment of damage and recovery of trees in Banksia-Casuarina woodland, burnt 1st February, 1959, as surveyed by students in July, 1959. All the trees in the transects, which were 1 chain wide, were counted and classified: saplings were counted separately from mature trees.

Transect	Species	Killed		Killed to ground level		Canopy stripped		Canopy intact	
		over 2m	under 2m	over 2m	under 2m	over 2m	under 2m	over 2m	under 2m
Transect 1 (7 sq. chains)	<i>Casuarina fraseriana</i>	9	22	3	139	261	7		
	<i>Banksia attenuata</i>	4	1	4	14	21	7	11	
Transect 2 (12 sq. chains)	<i>Casuarina fraseriana</i>	4	34	4	83	168	11	9	
	<i>Banksia attenuata</i>	3		10	24	103	3	2	
	<i>Banksia menziesii</i>	2	1	1	3	29		1	
A severe burn	Totals	22	58	22	263	482	28	23	
Transect 3 (5 sq. chains)	<i>Casuarina fraseriana</i>	3			24	9	3	77	
	<i>Banksia attenuata</i>				12	3		29	
A mild burn	Totals	3			36	12	3	106	

died but most of them survived. In February the root-stocks of some of them had a slight swelling of the hypocotyl. Two years later a small lignotuber, 8-10 mm in diameter had developed. By October 1960 surviving plants were still under 60 cm tall and lignotubers of two dug up were only 2.5 cm long and 1.5 cm diameter. Unfortunately a second fire in November 1954 had destroyed all except a few isolated plants near the fire edges so there was no chance to see what would have happened to such a dense stand of young plants. I have not seen an equivalent mass of seedlings since but similar mass germinations from early fires may explain thickets of *Casuarina* which occur in the park.

Banksia trees, with their very thick, very hard bark, suffer minimum damage to trunks of mature trees (Fig. 4A), though saplings are killed to ground level. Most trees sprout along the upper branches (Fig. 7E). Healthy shoots grow from the lignotubers of burnt-off saplings and seedling regeneration is good and well able to compensate for deaths of trees. After the severe fire in January 1973, a very large number of *Banksia* trees did not recover, but it is uncertain how many were dead or dying as a result of a long drought increasing the usual summer deaths. Another factor which could account for the high mortality in this extremely hot fire is destruction of the dense mat of proteoid roots which occurs close to the surface in the organic layer of the soil. Roots have been seen exposed on badly burnt sites.

The Eucalypts, *E. marginata* (Jarrah) and *E. calophylla* (Marri), both have rough bark which readily carries fire into the crown. Most of the Jarrah trees have scars at the base of the trunk which are burnt out more deeply with each successive fire. This is particularly bad where the trees are coppice from early cutting and debris collects between close trunks. Marri often does not show the extent of the damage until 3-4 years after the fire, when sheets of bark are pushed off by healing and growth at the side of the wound. This exposure shows how

much of the living cambium had been killed at the time of the fire, although the bark had not been burnt through (Fig 7G). In all the Eucalypts reduction of the crown through fire damage makes recovery from insect attack more difficult. Where upper limbs are killed they remain for many years projecting above the slowly growing branches from epicormics lower on the trunk. Figures 7A, B and C show a Jarrah tree before and after a bad fire in 1973 and Figure 7D one similarly damaged in a fire in February 1942, and photographed 18 years later. Few really healthy Jarrah trees remain.

The even more marked deterioration of Tuart trees in the park is due to a complex of factors of which fire is only one and perhaps a minor one. This has been discussed by Beard (1967).

Cycad

Macrozamia, with its large store of food in the underground (here) tuberous trunk, shows very rapid growth of the leafy crown which may be restored in one year. Cones are found, in plants old enough to reproduce, in the second year after a fire, but with slow development to seed-shed (about February-March) and a further year on the ground required to ripen the seed, seedlings will not appear until the fourth winter. Although the large seeds germinate on the surface of the ground, the tap root is strongly contractile so that the growing point of young plants is well buried and protected from fire.

Shrubs

As already reported, almost all of the shrubby undergrowth species are capable of sprouting when burnt off to ground level (Fig. 9). Of those few which are killed, several are tall shrubs which may reach small tree dimensions, e.g. *Dryandra sessilis*, *Conospermum triplinervium*, *Adenanthos cygnorum* (a few colonies only in King's Park—favoured habitat is very poor white sand), *Dodonea hackettiana* (confined to very small area). When old enough these may survive some fires though younger plants are killed as are the smaller species, *Acacia pulchella*, *Leuco-*

pogon racemulosum, *Calytrix fraseri*, *Pimelea rosea* and *Gompholobium tomentosum*. Seedling regeneration is good for all of these except *Leucopogon* and *Calytrix* where very few seedlings survive and the species are tending to become extinct, at least in the southern half of the park. All have the same habit characteristic of fire-sensitive species; a single main stem which continues into a tap root without enlargement below ground. Also each of these species continues to grow taller year by year and does

not sucker from the ground as do many of the sprouting species, even when not burnt.

The sprouting shrubs which, with the shrubby monocotyledons, make up the great bulk of the undergrowth, mostly have deep and massive woody tap roots, e.g. *Daviesia nudiflora*, *Oxylobium capitatum* (Fig. 8), in some cases enlarged into a true lignotuber, e.g. *Persoonia saccata*. Many others have somewhat similar but more irregular and less deep and massive woody root



Figure 7.—Trees. A, B and C show the same jarrah tree. A.—Photographed in 1960. B.—Soon after the severe fire in January 1973. C.—More than a year later April 1974. The upper part of the tree had not recovered, the base of the trunks were clothed with epicormic shoots. D.—A jarrah similarly damaged by a fire in February 1942, and photographed November 1959. Two of the now 18 year old branches can be seen on the right side of the tree, those on the left fork are obscured by the better foliage of a sapling in front. E.—A less severely burnt jarrah tree in which the canopy is recovering. The smaller Banksias in the background show similar sprouting in the upper branches. Burnt January 1970, photo April 1970. F.—A marri which was a fine shapely tree before a fire from which it has not fully recovered; veld grass became established after the same fire. G.—The scarred trunk of a marri tree burnt 3 years earlier and photographed when the killed bark had just fallen exposing the damage and growth at the edge of the scar.



Figure 8.—Root system. A.—Young plants of a species capable of sprouting (*Oxylobium capitatum*) and one which is killed by fire (*Gompholobium tomentosum*). *Oxylobium*, even at this early stage, has a much thicker and longer (broken off in specimen) root in proportion to its top than *Gompholobium*. B.—Rootstock of an old plant of *Daviesia nudiflora* which has been repeatedly burnt.

systems, e.g. *Bossiaea*, *Hibbertia*, *Astroloma*, or somewhat fleshy ones, as *Scaevola* spp., *Helichrysum cordatum*. *Hardenbergia*, a climber with particularly deep thick tap roots, regenerates extremely rapidly and grows through the summer. Suckering from horizontal roots is not uncommon and results in concentrations of plants in species with this habit, e.g. *Stirlingia*, *Grevillea vestita*, *Acacia stenoptera*, *Macarthuria* and others.

Many of these plants are undoubtedly very long-lived. Unfortunately there are no conspicuous annual rings by which to date them, but some indication has been given in quadrats kept under observation since 1936 or 1940 (Appendix 1). In one quadrat laid down in 1936, the same plants of *Daviesia nudiflora*, *D. juncea* (1 died) *Hibbertia hypericoides*, *Hypocalyymma robusta*, are still there in 1973 (37 years), and not very different in size. One of the observed characteristics of unburnt shrub species is the relatively small annual growth increments and the death of some branches over the summer. In other long-term quadrats the same plants of *Leucopogon propinquus*, *Petrophile macrostachya*, *Mesomelacna stygia* and *Stirlingia* are still surviving. All these quadrats have been burnt several times during the 30 or more years since they were first mapped. Although *Persoonia* was not in any of these quadrats, the size of some lignotubers suggests that it is very long-lived. It would be interesting to know whether the life span of some of these shrubs equals or exceeds that of some of the trees.

The pattern of regrowth for these shrubs is rapid growth of erect multiple shoots from a

few cm below ground level so that the plants are almost back to their pre-fire size in 2 or 3 years or less. Thereafter, growth becomes slower and slower and flowering is reduced.

Stirlingia is rather distinctive. The vigorous growth and abundant production of tall flowering panicles makes this the dominant shrub (in stands where it occurs) for its first flowering after a burn (Fig. 11). In the following year 2 lateral branches grow from below the old fruiting panicle and in subsequent years these continue to grow without flowering and with decreasing stem increments and decreasing leaf size.

Some of the smaller semi-herbaceous perennials, e.g. *Macarthuria*, *Hybanthus ealycinus*, *Monotaxis grandiflora* and *Opercularia*, also able to shoot from below ground level, have survived repeated fires well although lacking massive rootstocks. There is a zone of soft corky tissue about ground level on the slender stems or roots which may give some insulation against fire as well as against summer soil heat.

Species which have disappeared from or have been greatly reduced in some frequently burnt areas are *Pimelea leucantha*, *Calytrix flavescens* and *Cryptandra arbutiflora*. These sprout weakly but succumb to repeated fires. *Phyllanthus* and *Hovea* have decreased in abundance in frequently burnt areas, although both regenerate after fire from sprouting and from seedlings. *Hovea* has gone from 2 permanent quadrats. Numerous seedlings had become established after fires before, but not since the quadrats were overgrown by veld grass. Competition from veld grass may be a factor in the decline of these two probably not particularly long-lived species.

Seedling regeneration of long-lived species need not be frequent but is still necessary. Seedlings of *Oxylobium*, *Hovea*, *Daviesia nudiflora*, *Jacksonia* spp., *Hardenbergia* and *Phyllanthus* are frequent and not only after fires. *Hibbertia hypericoides*, one of the commonest species in the park, produces very few seeds and seedlings are extremely rare. In *Stirlingia latifolia*, which has prolific seeding after fire, seedlings are also very rare, but in this species there is highly efficient vegetative multiplication.

Persistent evergreen geophytes

The harsh sedges and some of the *Xanthorrhoeaceae* with massive underground parts and buried and well-sheathed growing apices are probably the most fire-resistant plants in the community. They are the first to show recovery after fire and the most persistent in repeatedly burnt areas.

Xanthorrhoea preissii is generally accepted to be a very slow-growing long-lived species though there is little factual record. In the repeatedly burnt Banksia woodland the plants are mostly tufts of leaves from the ground with little, if any, stem above ground level. Fire damage seems to produce multiple growing apices. How much of the absence of tall specimens here is due to conditions, or how much is due to cutting for



kindling before the park was reserved—100 years ago—is largely speculation. There are some specimens with trunks up to about 2 m in the Tuart and limestone sections. An undisputed fact is that burning induces profuse flowering (Fig. 3F) the first year after a burn. The dry fruiting spikes persist for another year or more.

The sedges, *Tetrariopsis octandrus*, *Mesome-laena stygia*, *Lepidosperma* spp., *Schoenus grandiflora*, form massive clumps (particularly below ground) with well-sheathed and buried growing apices. Plants of these have persisted in quadrats observed for 30 years or more but no doubt live very much longer than this. Plants vary in size from single tufts to clumps covering circular areas up to 60 cm diameter. *Amphipogon turbinatus* is a grass with a similar harsh bushy habit and underground rhizomes. Rhizomatous species of *Restio* and *Loxocarya* are widespread and also extremely fire-tolerant. *Lomandra* species have underground growing points well sheathed by persistent leaf bases, and *Thysanotus sparteus*, a leafless inconspicuous plant above ground, has a short thick rhizome buried up to 6–10 cm below ground level.

Herbaceous geophytes and other perennial species which die down over summer

These are very different: mostly small plants; orchids, sundews (*Drosera* spp.), trigger plants (*Stylidium* species) and small liliaceous species. Although over 40 have been recorded, many are rare and inconspicuous. All are active only from the period of the first effective rains until the upper layers of the soil dry out in early summer. They tolerate fires well as they have usually died down to the dormant subterranean stage before the fire. As stated earlier, they benefit particularly from autumn fires when the shrub competition is most reduced. The common and widespread species, *Burchardia umbellata*, flowers in unburnt bush, but flowers are more abundant and more conspicuous in burnt areas. *Haemodorum* (2 species) produces tall robust spikes (Fig. 3F) from deep, massive, well-sheathed growing points. The trigger plant, *Stylidium carnosum*, and the orchid, *Prasophyllum elatum*, also produce tall spikes rarely seen except after fire. Neither is common. Many of the orchids flower better but not exclusively after fires. This is true of the most common species of orchids, *Caladenia flava* and *Diuris longifolia*, and also of *Eryngium pinnatifida* (Umbelliferae). The rosette *Stylidium brunonianum* and *S. piliferum* deserve a special mention as they have no underground perennating organs but survive both fire and summer drought with the small dry leaves closed over the growing point. There is only one minor grass, *Micro-laena stipoides*, in the herbaceous rhizome geophyte category.

Annuals

Most of the park annuals appear to be larger and more floriferous after fires. *Podotheca chrysantha* showed this markedly after several late summer fires. The small umbelliferous species, *Trachymene pilosa* and *Homalosciadium homalocarpum* increase in abundance, although always present, but *Calandrinia corrigioloides* and *C. liniflora* are rarely seen except after fires when the former particularly is extremely abundant. The occurrence of all of these annuals is uneven at any time and no doubt their presence and abundance in any particular place after fire is related to the amount of seed in the ground. A fire occurring before annuals had set seed could be detrimental. The only spectacular true 'fireweed' among the annuals is *Stipa compressa*. This species, flowering in October and striking with its long golden awns, is normally abundant and widespread in the first year after a fire and completely absent the following year, although there has been little change in the habitat, and there must be seed in the ground as the grass appears again in abundance after another fire.

Introduced species

Veld grass

The tremendous spread and increase of veld grass (*Ehrharta calycina*) over the past 20–30 years has been reasonably well documented. Its increase after fires has been noted repeatedly. A photographic record of a first appearance after a fire is shown in Figure 10. Several of the permanent quadrats were put down either before or shortly after veld grass invaded them and show its history in each quadrat. Increase after fire is shown in quadrat A3 (Appendix 1, Fig. 13). In all quadrats very numerous seedlings were noted after fires although sometimes old moribund clumps were killed. These quadrat samples are small and lately near widening road verges. All remaining plots have been for many years overgrown with veld grass.

The relation to fire is partly an indirect one, since the edges of annually ploughed firebreaks provide a particularly favourable habitat for the establishment of veld grass. The spread along and into the bush from firebreaks was shown in an extensive survey by Watson and Meagher in 1949. A re-survey by them of part of the area 8 years later confirmed the relation to firebreaks and showed a further spread and increase in density of the grass. However, another section remapped in 1961, and which had been free from fire since 5 years before the earlier mapping, showed a very significant decrease in contrast to an adjacent portion which had been burnt and showed an increase. In one quadrat, unburnt for 15 years, there had been a gradual decrease from 115 clumps to 6 clumps in the

Figure 9.—Examples of shrub regrowth. A, B, F, G in the first year. C, D, E after several years. A.—*Petrophile macrostachya*—regrowth in March after a December burn. B.—*Leucopogon propinquus* regrowth 6 months after a July burn. C.—Unburnt *Pimelea* a species which regenerates weakly and is tending to disappear. D.—*Conospermum triplinervium*. Young plants which grew from seed after a fire which killed the parents, flowering for the first time in their seventh year. E.—An unburnt *Petrophile macrostachya* in flower. F.—*Stirlingia latifolia* 6 months after a December burn, in bud on short regrowth. G.—*Scaevola canescens* regrowth 6 months after a March burn.

36 m². On the western edge of the park, where *Banksia-Casuarina* canopy was dense, there was negligible penetration of the veld grass into unburnt bush, in spite of its occurrence along the cleared boundary. In a different site, where shrub undergrowth was dense but tree canopy poor, as a result of severe but infrequent fires, there was also very little veld grass. These

examples and other general observations show that undisturbed dense bush can resist the advance of veld grass and even suppress it. As a contrast, in a section of University land burnt almost annually from 1950, veld grass spread from a cleared section and by 1960 most of the site was becoming a veld grass savannah woodland. In general, veld grass has increased more rapidly in the open Tuart woodlands than in the dense Jarrah-*Banksia-Casuarina* communities.

Other introduced species

Introduced bulbs, e.g. *Gladiolus* and Cape Tulip, so much more massive than the native herbaceous geophytes and with enormously greater seed production, have also been spreading through the park in recent years, particularly in areas burnt or mown, and are likely to constitute another hazard for the indigenous vegetation. Figure 3A-C shows how much bare sand is open to colonisation by weeds after a summer fire.

It should be mentioned that there are annual weeds which have been long established throughout the bush, e.g. *Ursinea anthemoides*, *Heliochloa pusilla*, *Kohlrachia prolifera*, *Briza maxima* and some other grasses and medics. In the poor sandy soil these plants remain very small and constitute no threat to the indigenous vegetation. There is often a temporary increase in size after fire but the effect is not lasting. In disturbed areas numerous species of weeds are flourishing.

In the south west corner of the park there has been a gradual spread, a short distance into the bush, of *Agonis flexuosa* from trees planted along a road near the beginning of the century. This is a species native to the Perth coastal plain, though not naturally present in this area. Fires may have aided this spread but no records have been kept.

Discussion

It has been shown that few plants are killed by fire. In the Jarrah-*Banksia-Casuarina* woodland none of the persistent monocotyledons are fire-sensitive and only 8 of the 90 species of the dicotyledon trees, shrubs and undershrubs. When the woody species more or less confined to the Tuart and limestone sites are included, another 8 fire-sensitive shrubs can be added. Fire-sensitive shrubs are marked (F) in the species list (Appendix 2).

A striking feature is the speed of the recovery of the undergrowth. The rapid growth of long, sturdy multiple shoots of the sprouting shrubs contrasts with the relatively small annual growth increments in unburnt bush. In the early stages of regrowth after fire the still intact deep and extensive root systems are supplying small shoots, and the greatly reduced total transpiration of the vegetation means more water remaining in the soil. Thus growth of the new shoots can be faster and continue longer into the summer than growth of the same species in unburnt bush. This advantage applies only to



Figure 10.—Veld grass. A.—Veld grass well established having spread after fire in 1958 from the firebreak in the foreground, November 1960. B & C.—The same site: B in October 1956 with dense shrub cover and C in October 1960 after a fire in January 1958 in which one of the 4 marri trunks was burnt through and fell (lying across right of photograph); veld grass established and flowering; marri coppice from base of trees.

the deep rooted plants. For shallow rooted species conditions on burnt areas are more severe in early summer because of earlier drying out of the exposed surface soil.

The rapid growth of shoots from old root systems is in contrast with the very slow growth of seedlings of the same species. In some sites observed, seedlings of *Phyllanthus*, *Bossiaea*, *Daviesia nudiflora*, *Oxylobium* were mostly only 10 cm or less in the first year, and a few up to 30 cm but most less than 20 cm in the second year. The tap roots were very much longer than the shoots and most seedlings showed a corky thickening in the surface layer of soil. The very small top no doubt enables the plant to survive the summer until the root is well established. Under favourable conditions, as under cultivation, growth is very much faster.

These observations confirm the adaptation to fire of this vegetation and both its inherent stability and its vulnerability to disturbance.

The stability is shown in the periodic rejuvenation and long survival of individual plants through repeated fires; the abundant renewal from seed of some of the fire-sensitive species and in the resistance of healthy undisturbed bush to aliens. The fact that most species in the undergrowth are long lived, slow growing but sprouting vigorously from ground level after fire makes for a stable population with the same major species occupying the same sites. The relatively few perennial species killed, but regenerating freely from seed after fire, show much more variable and fluctuating populations as seeds and seedlings are more susceptible to hazards of weather and to destruction by insects.

The vulnerability is exhibited in the general deterioration of the bush, the deformed and stagheaded trees, the reduction of many of the attractive species, and the over-running of the area by veld grass and to a lesser extent by other aliens. Too frequent and too severe fires are undoubtedly contributing but not the only factors responsible. It seems clear that the effect of introduction of a perennial grass such as *Ehrharta calycina* has been to change the whole cycle of regeneration after fires. Herbaceous species with extensive root systems are more or less lacking in the undisturbed bush; annuals are small and short-lived and are dried off before any severe water stress for perennials; herbaceous geophytes are small and non-aggressive. Both categories probably contribute a little easily decomposed organic matter to the surface layers of soil but are neither large enough nor numerous enough to offer any serious competition even to the seedlings of woody shrubs and certainly not to the adult plants. It is very different with *Ehrharta* which so thoroughly exploits the soil with roots which penetrate deeply as well as ramifying through the upper levels.

Although mature shrubs have persisted in dense veld grass and have even been able to suppress it, survival of seedlings is much more difficult. There is some evidence for this sug-

gestion from permanent quadrats (see Appendix 1). For example, in H3 (Fig. 12) after the fire in summer 1936-37, there were very numerous seedlings of the fire-sensitive *Gompholobium* and *Acacia pulchella*, also several of the regenerating *Hovea* and *Helichrysum cordatum*. None of these have been recorded since the quadrat has been covered with veld grass. In A3 (Fig. 13), in 1947, a group of young *Daviesia nudiflora* plants established from seedlings after fire in 1944 were reduced in 1951 to a single plant which had gone by 1954. Veld grass was well established before 1951. Seedlings of *Daviesia nudiflora* have not been recorded in this quadrat since. Another quadrat free of veld grass had, until 1954, numerous young plants, many originating after a fire in 1942; unfortunately, it was destroyed in 1954 soon after the first entrance of veld grass.

No records have been kept of numbers of annuals but general observation is of reduction where veld grass is dense. However, annuals are suppressed also by the native shrubs and are only abundant after fire and in more or less open spaces.

Deliberate use of fire

Records of regeneration after fires in different seasons and at different intervals give some guidance to possible management by controlled burning.

Given a healthy stand without veld grass or South African bulbs, a good tree canopy with predominantly herbaceous undergrowth could be maintained by frequent mild autumn burns, perhaps every 4 or 5 years. Towards the end of the dry season herbaceous geophytes are dormant with their perennating parts fully mature, annuals are dead with seeds dry and hard. A light autumn burn provides a good seed bed, with increased minerals and increased spaces free from smothering shrubs and leaf litter, so that conditions are ideal when the rains start.

On the other hand, the common flowering shrubs such as *Hibbertia*, *Daviesia*, *Oxylobium* and *Hypocalymma* may be encouraged by spring or early summer burns which give them a good start before the next winter rains bring up the herbs which then have to face strong competition from the shrubs. Seeding of the previous season's annuals may have been prevented by early fire. As mentioned earlier many of the sprouting shrubs require periodic burning to keep them in healthy flowering condition. Periodic burning also maintains young and vigorous colonies of the freely seeding fire-sensitive species, *Acacia pulchella*, *Gompholobium tomentosum* and *Pimelea rosea* but for these it is essential that enough time elapses between fires for the new plants to produce seed. Stands burnt at intervals of about 8-10 years have maintained good shrub cover. Shorter intervals favour some species, longer others. For successful establishment of trees and long lived shrubs, it is probably the intensity of the fire which determines the age necessary for survival, certainly many small saplings have been killed in summer fires; another argument for mild

control burns. Figure 11A-B contrasts the damage resulting from a successful control burn and a severe wildfire.

Where *Banksia-Casuarina* canopy is dense, complete or long term protection of some small areas would preserve some of the more vulnerable species and produce a type of woodland in which the shrub layer is suppressed so that the space between ground and tree canopy is more open.

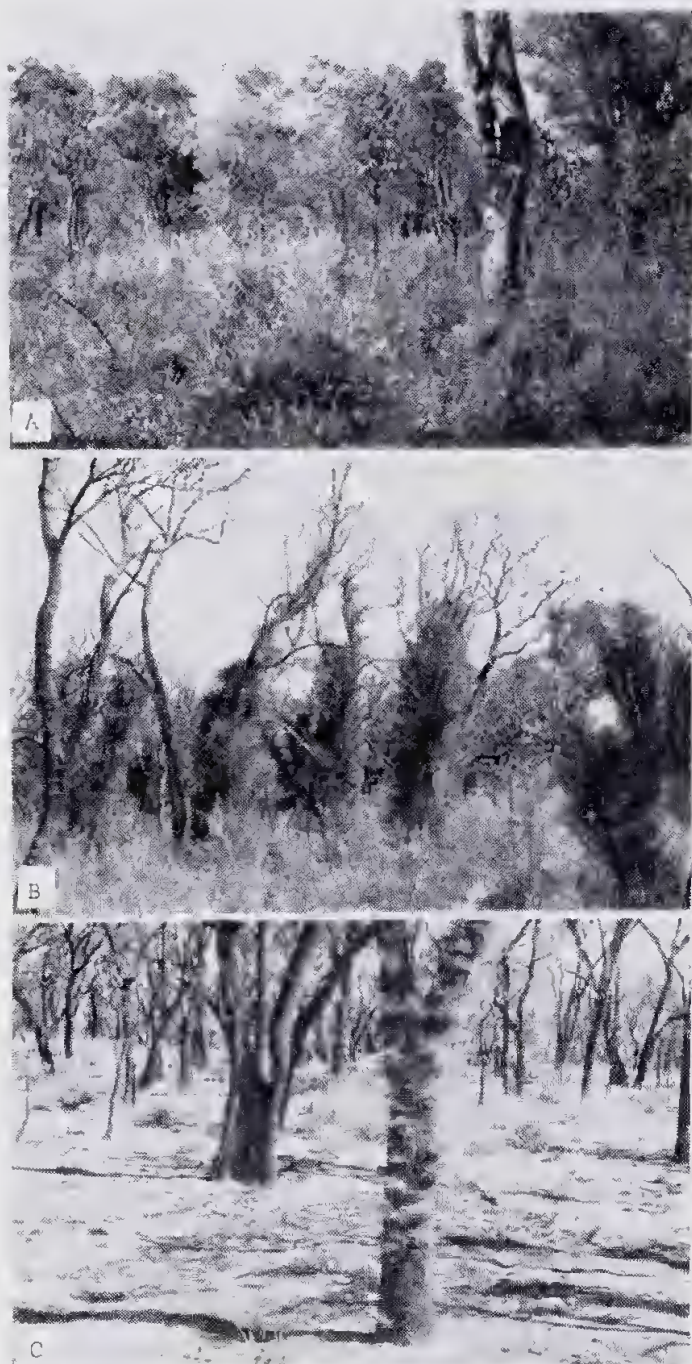


Figure 11.—Contrasting results of control burning and wildfire. A.—Nine months after a successful control burn; young trees undamaged, good shrub cover re-established. B.—Eighteen months after a wildfire in January 1973; no recovery of tops of trees; *Casuarina* trunks clothed in epicormics; *Stirlingia* flowering in both photographs. C.—Early stage of epicormic growth on *Casuarina* trunk; another tree scarred by a previous fire with growth at the edge of the old wound showing.

By burning small areas at a time, stands of the above types in different stages of regeneration could be maintained to give a pleasing variety as well as some protection against wild fires. Unfortunately the present condition of poor trees and veld grass through most of the undergrowth makes the position much more difficult. Nevertheless, the known facts of the effects of fire allow some measure of control at least in the areas less badly infested with weed species.

Further research

There is a big field of research in understanding the differing responses of different species to burning. In other parts of the world, e.g. the Californian chaparral (as well as Australia) abundance of particular species after fires has been related to different causes, some inherent in the morphology of plant or seed, others response to the changed environment. Some indications which could be followed up in species from King's Park are given.

Species of *Daviesia* and *Stirlingia latifolia* grow and flower after fire as do plants in the undisturbed bush cut to ground level. The pruning effect of fire seems to be the main influence here as the habitat is unchanged. Fasciated shoots have been found on fire regrowth, most commonly in the legumes, *Daviesia* spp., and *Jacksonia* spp. Is this a response to wounding or to unbalanced nutrition? With *Persoonia saccata* the particularly strong regrowth is understandable as it has the most massive lignotuber of any shrub species in the park. The regrowth apparently flowers only when it has reached a certain size level or maturity irrespective of season. If unburnt, it flowers only in December. It is apparently indifferent to day length and temperature. By contrast *Stirlingia latifolia* flowers in September whenever it is burnt, although the vegetative shoots are very much taller where the interval between fire and flowering is longer. This does suggest a day length control. Why doesn't it flower unburnt? *Kennedia prostrata*, both regrowth and seedlings, always grows better on or near ashbeds; extra potassium in the soil may be a factor.

Among the monocotyledons very striking flowering of the *Xanthorrhoea* occurs in the first year after a fire. Flowering is very rare in unburnt bush, but does occur in gardens receiving extra water and fertiliser. Similarly, in the cycad *Macrozamia*, coning occurs more frequently in gardens.

Examples of 2 sedges with different responses are *Tetraropsis octandrus* which produces stiff erect flowering shoots very quickly after a burn; thereafter the leaves continue to grow on with no flowering until, in long-unburnt bush, mats of long trailing leaves spread over the ground. In *Lepidosperma* species, on the other hand, new flowering stems are produced from the base each year, burnt or unburnt.

How is it that the seed of *Stipa compressa* can be in the ground through so many wet winters without germinating and then grow so luxuriantly after a fire? The stand of Figure 3 had not been burnt for 13 years. Seeds of other species of *Stipa* in the arid inland survive drought, and germinate following good rains.

The ecology and physiology of species in this environment where fires are frequent offer scope for interesting research. It is, however, important that the normal growth habits, which are very varied, and responses to differing annual weather patterns, are known before detailed study is undertaken on responses to fire.

Acknowledgments.—Acknowledgments are difficult as so many workers have been interested in King's Park for many years and have talked with me about it. Quantitative work was initiated by Dr. J. I. Armstrong in 1936 as student exercises and has been continued since by successive generations of students and staff. A considerable body of information has been built up on the distribution and abundance of species. I have

used a few samples of old quadrats as related to fire history and part of a student survey of tree damage by fire.

Permission to work in the park, and helpful interest, has been given by successive directors and superintendents. I wish to thank Mr. J. E. Watson particularly, for records of burning and of the invasion of veld grass in the park during his term of office. I have included repetition of notes on fires which I provided for the paper by Main and Serventy (1957) already referred to.

A species list has been in use in the Botany Department of the University of Western Australia for many years and from time to time has been updated with the help of the staff of the Western Australian Herbarium. Specimens from King's Park held in the Botany Department, University of Western Australia, go back as far as 1917.

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Main, A. R. and Serventy, D. L. (eds.) (1957).—King's Park as an indigenous park—A natural history appraisal. *W.A. Naturalist* 6: 25-33.

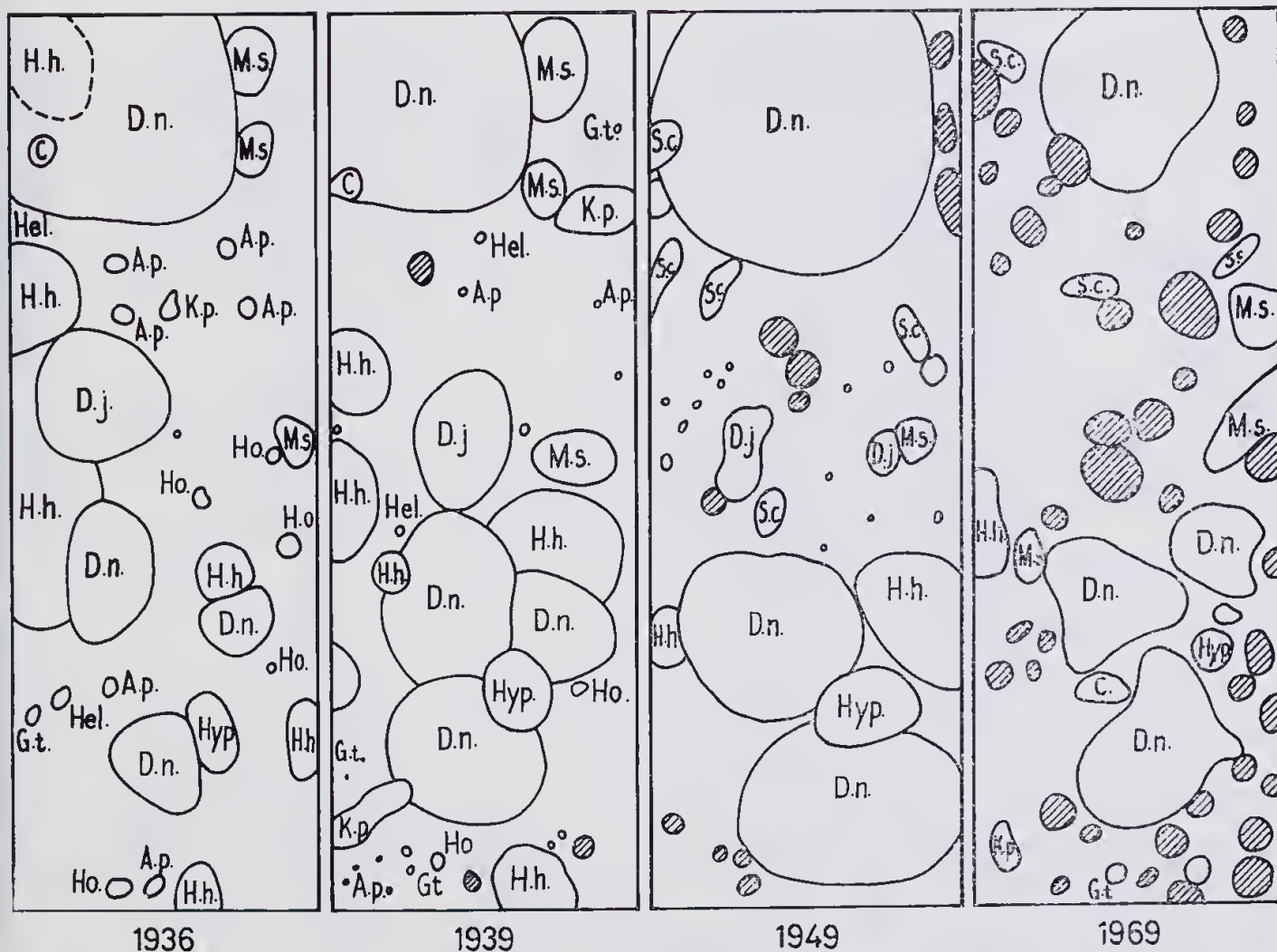


Figure 12.—Quadrat H3. First mapped in 1936, burnt in November 1936, November 1944, grazed by cows in 1951, burnt again in December 1960, and mown in 1966. First appearance of veld grass 1939 with large numbers of seedlings after the 1944 fire and after grazing. In 1953 old plants were waning in vigour but were abundant again 2 years after the 1960 fire. The same plants of *Daviesia nudiflora*, *D. juncea*, *Hibbertia hypericoides*, *Hippocalymma robusta*, and *Mesomelaena* have persisted more or less unchanged for over 30 years. There has been some loss in total shrub numbers. Seedlings of *Acacia pulchella* *Gompholobium*, *Hovea* and *Helichrysum* were abundant after the 1936 fire but surviving seedlings have been few since the veld grass overran the quadrat.

APPENDIX 1

Quadrats

Examples are given of a few of the chartings of two of the long standing quadrats H3 (Fig. 12) and A3 (Fig 13), both in predominantly Banksia-Casuarina woodland although there was an old tuart stump in A3 (not in the strip shown). The quadrats were 6 yards x 6 yards (approx. 6 x 6m) but for simplicity only one 6 x 2 m strip is reproduced. Shrubs and woody monocotyledons only were recorded of the native species, but because of the interest of the invading veld grass that was recorded, the outlines representing the basal area of the clump, not the trailing foliage which spreads over most of the quadrat in later stages of its invasion.

Symbols used for species in quadrat charts

A.p.—*Acacia pulchella*; C.p.—*Conostephium pendulum*; C.pr.—*C. preissii*; C.c.—*Conostylis*

candicans; C.s.—*C. setigera*; D.j.—*Daviesia juncea*; D.n.—*D. nudiflora*; D.l.—*Dianella revoluta*; G.t.—*Gompholobium tomentosum*; Hel.—*Helichrysum cordatum*; H.h.—*Hibbertia hypericoides*; H.H.—*H. huegclii*; H.r.—*H. racemosa*; Ho.—*Hovea trisperma*; Hyp.—*Hypocalymma robusta*; H.c.—*Hardenbergia comp-toniana*; J.g.—*Jacksonia gracilis*; K.p.—*Kennedia prostrata*; L.p.—*Leucopogon propinquus*; Le.—*Lepidosperma* sp.; M.S.—*Mesomelaena stygia*; O.c.—*Oxylobium capitatum*; P.c.—*Phyllanthus calycinus*; R.—*Restio nitens*; S.c.—*Scacvola canescens*; S.p.—*S. paludosa*; St.—*Stirlingia latifolia*; Syn.—*Synaphaea polymorpha*; Tri.—*Trichoryne elatior*; X.—*Xanthorrhoea preissii*; / / / *Ehrharta calycina* (veld grass), outline shows basal area of clump.

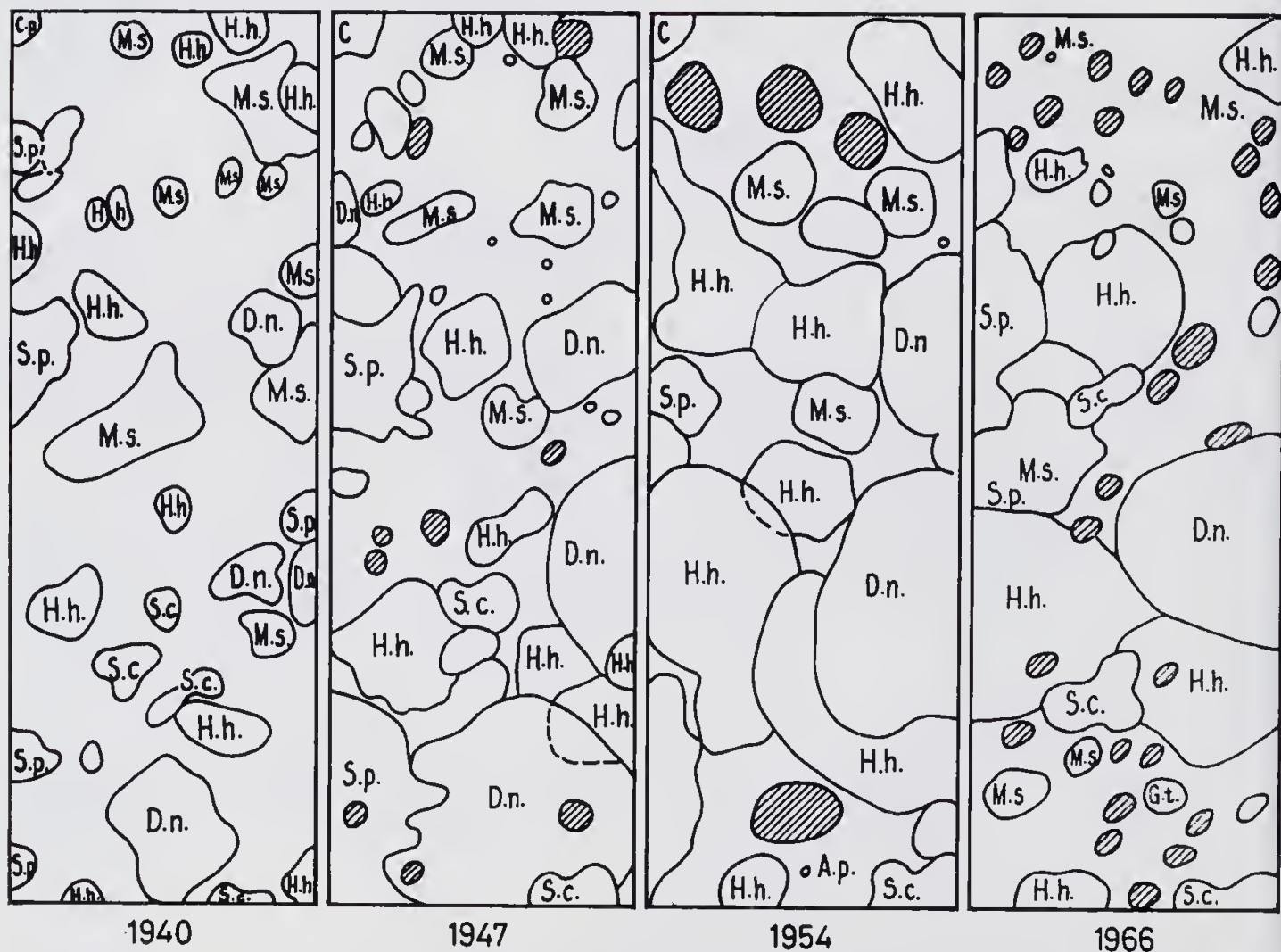


Figure 13.—Quadrat A3. Burnt in April 1939 and first mapped in August 1940. It was burnt again in April 1942, November 1944, November 1954, December 1958, mown December 1963. Three fires in close succession then a 10 year interval. Veld grass first appeared in 1945 and was well established by 1947. The same plants of *Daviesia nudiflora*, *D. juncea*, *Hibbertia hypericoides*, *Leucopogon propinquus*, *Stirlingia latifolia*, *Scaevola canescens*, *Mesomelaena stygia* have persisted throughout the period.

APPENDIX 2

King's Park species list

Species marked (L) are more or less confined to soils with limestone underlying or outcropping. Species marked (a) are annuals. (F) denotes species which are killed by fire, all others are capable of sprouting from burnt stems or roots.

Cycadaceae

Macrozamia riedlei (Gaud.) C. A. Gardn.

DICOTYLEDONS

Aizoaceae

Macarthuria australis Hueg.

Amarantaceae

Ptilotus polystachyus (Gaud.) F. Muell.

P. drummondii (Moq.) F. Muell.

Casuarinaceae

Casuarina fraseriana Miq.

C. humilis Otto & Dietr.

Chenopodiaceae

L *Rhagodia baccata* (Labill.) Moq.

Compositae (Asteraceae)

a *Angianthus humifusus* (Labill.) Benth.

a *Athrixia pulverenta* (Lindl.) Druce.

Helichrysum cordatum DC.

Lagenifera huegelii Benth.

a *Milotia tenuifolia* Cass.

L *Olearia axillaris* (DC.) F. Muell.

a *Podosperma angustifolium* Labill.

a *P. chrysanthum* (Steetz) F. Muell.

a *Podolepis nutans* Steetz.

a *Quinetia urvillei* Cass.

Senecio lautus Forst. f. ex Willd.

a *Waitzia citrina* (Benth.) Steetz.

a *W. suaveolens* (Benth.) Druce.

Crassulaceae

a *Crassula colorata* (Nees) Ostenf.

Dilleniaceae

Hibbertia huegelii (Endl.) F. Muell.

H. hypericoides (DC.) Benth.

H. racemosa (Endl.) Gilg.

Droseraceae

Drosera erythrorhiza Lndl.

D. glanduligera Lehm.

D. menziesii R. Br.

D. stolonifera Endl.

Epacridaceae

Astroloma ciliatum (Lindl.) Druce.

A. macrocalyx Sond.

A. pallidum R. Br.

Conostephium pendulum Benth.

C. preissii Sond.

L *Leucopogon parviflorus* (Andr.) Lindl.

L. propinquus R. Br.

F *L. racemosus* DC.

Euphorbiaceae

Monotaxis grandiflora Endl.

Phyllanthus calycinus Labill.

Ricinocarpus glaucus Endl.

a *Poranthera microphylla* Brongn.

Geraniaceae

Pelargonium capitatum (L.) Ait.

Goodeniaceae

Dampiera linearis R. Br.

Lechenaultia floribunda Benth.

Scaevola canescens Benth.

S. holosericea De Vriese.

L F *S. nitida* R. Br.

S. paludosa R. Br.

L *S. thesioides* Benth.

Haloragaceae

Glischrocaryon aureum (Lindl.) Orchard.

Haloragis pithyoides (Nees) Benth.

Lablatae (Lamiaceae)

Hemiandra pungens R. Br.

Lauraceae

L *Cassytha racemosa* Nees.

Mimosaceae

Acacia cyclops A. Cunn. ex G. Don.

A. diptera Lindl.

A. heteroclita Melsn.

A. huegelii Benth.

F *A. pulchella* R. Br.

A. saligna (Labill.) H. Wendl.

Papilionaceae (Fabaceae)

Bossoaea eriocarpa Benth.

Daviesia divaricata Benth.

D. juncea Sm.

D. nudiflora Melsn.

D. pectinata Lindl.

L *Gompholobium aristatum* Benth.

F *G. tomentosum* Labill.

Hardenbergia comptoniana Benth.

Hovea trisperma Benth.

Isotropis cuneifolia (Sm.) Domin.

Jacksonia furcellata (Bonpl.) DC.

J. gracilis Melsn.

J. sternbergiana Hueg.

Kennedia prostrata R. Br.

Oxylobium capitatum Benth.

L *Templetonia retusa* (Vent.) R. Br.

Lobeliaceae

a *Lobelia tenuior* R. Br.

Loranthaceae

L *Amyema miquelii* (Lehm. ex Miq.) Tiegh.

Nuytsia floribunda (Labill.) R.Br.

Myoporaceae

L *Eremophila glabra* (R.Br.) Ostf.

L *Myoporum insulare* R.Br.

Myrtaceae

Agonis flexuosa (Spreng.) Schau.

Calytrix angulata Lindl.

C. flavesceus A. Cunn.

F *C. fraseri* A. Cunn.

L *Calothamnus quadrifidus* R.Br.

Eremaea pauciflora (Endl.) Druce.

Eucalyptus calophylla R.Br.—Marri.

L *E. gomphocephala* D.C.—Tuart.

E. marginata Sm.—Jarrah.

Hypocalymma robusta Endl.

Kunzea ericifolia Reichb.

L *Melaleuca accrosa* Schau.

L *M. huegelii* Endl.

Phytolaccaceae

Tersonia brevipes Moq.

Pittosporaceae

L *Sollya heterophylla* Lindl.

Polygalaceae

Comesperma calymega Labill.

L *C. confertum* Labill.

Portulacaceae

a *Calandrinia corrigioloides* F. Muell. ex Benth.

a *C. liniflora* Fenzl.

Proteaceae

F *Adenanthos cygnorum* Diels.

Banksia attenuata R.Br.

B. grandis Willd.

B. ilicifolia R.Br.

B. menziesii R.Br.

B. prionotes Lindl.

Conospermum stoechadis Endl.

L F *C. triplinervium* R.Br.

Dryandra nivea R.Br.

D. sessilis (R.Br.) Druce.

L F *Grevillea crithmifolia* R.Br.

L *G. thelemanniana* Hueg.

- L *G. vestita* (Endl.) Meisn.
 L F *Hakea lissocarpa* R.Br.
H. prostrata R.Br.
 L F *H. trifurcata* (Sm.) R.Br.
Persoonia saccata R.Br.
Petrophile linearis R.Br.
P. macrostachya R.Br.
 L *P. serruriae* R.Br.
Stirlingia latifolia (R.Br.) Steud.
Synaphaea spinulosa (Burm. f.) Merrill.

Ranunculaceae

- L *Clematis microphylla* DC.

Rhamnaceae

- L *Cryptandra arbutiflora* Fenzl.
 L F *Spyridium globulosum* (Labill.) Benth.
S. tridentatum (Steud.) Benth.
 L F *Trymalium ledifolium* Fenzl.

Rubiaceae

- Opercularia vaginata* Labill.

Rutaceae

- L *Boronia ramosa* (Lindl.) Benth.
Eriostemon spicatus A. Rich.

Solanaceae

- L F *Anthocercis littorea* Labill.

Stackhousiaceae

- Stackhousia brunonis* Benth.

Sapindaceae

- F *Dodonaea hackettiana* W. V. Fitzg.

Sterculiaceae

- L *Thomasia cognata* Steud.

Stylidiaceae

- Stylidium brunonianum* Benth.
 a *S. calcaratum* R.Br.
S. carnosum Benth.
S. piliferum R.Br.
S. repens R.Br.
S. schoenoides DC.

Thymelaeaceae

- F *Pimelea rosea* R.Br.
P. sulphurea Meisn.
P. leucantha Diels.

Umbelliferae (Apiaceae)

- Eryngium pinnatifidum* Bunge.
 a *Homalosciadium homalocarpum* (F. Muell.) Hj.
 Eichler.
 a *Trachymene pilosa* Sm.
Xanthosia huegelii (Benth.) Steud.

Violaceae

- Hybanthus calycinus* (DC. ex Ging.) F. Muell.

MONOCOTYLEDONS

Centrolepidaceae

- a *Centrolepis drummondii* (Nees) Hieron.

Cyperaceae

- Lepidosperma angustatum* R.Br.
 L *L. gladiatum* Labill.
L. resinosum (Nees) Benth.
L. scabrum Nees.
Mesomelaena stygia (R.Br.) Nees.
Schoenus curvifolius (R.Br.) Benth.
S. grandiflorus (Nees) F. Muell.
 a *Scirpus antarcticus* L.
S. arenarius Benth.
Tetrariopsis octandra (Nees) C. B. Clarke.

Gramineae (Poaceae)

- Amphipogon turbinatus* R.Br.
Danthonia semiannularis (Labill.) R.Br.
 L *Dichelachne crinita* Hook.
Microlaena stipoides (Labill.) R.Br.
Neurachne alopecuroides R.Br.
 a *Stipa compressa* R.Br.
 L *S. elegantissima* Labill.
S. hemipogon Benth.
S. variabilis Hughes.

Haemodoraceae

- Anigozanthos humilis* Lindl.
A. manglesii D. Don.
Conostylis aculeata R.Br.
C. candicans Endl.
C. setigera R.Br.
Haemodorum paniculatum Lindl.
H. spicatum R.Br.
Phlebocarya ciliata R.Br.

Iridaceae

- Orthrosanthus latus* (Endl.) Benth.
Patersonia occidentalis R.Br.

Juncaceae

- Luzula meridionalis* Nord.

Liliaceae

- Agrostocrinum scabrum* (R.Br.) Bail.
Arnocrinum preissii Lehm.
Arthropodium preissii Endl.
Burchardia umbellata R.Br.
Caesia parviflora R.Br.
Corynotheca micrantha (Lindl.) Macbride.
Dianella revoluta R.Br.
Laxmannia squarrosa Lindl.
Sowerbaea laxiflora Lindl.
Tricoryne elatior R.Br.
Thysanotus arenarius N.Br.
T. patersonii R.Br.
T. sparteus R.Br.
T. thyrsoides Baker.
T. triandrus (Labill.) R.Br.

Orchidaceae

- Caladenia deformis* R.Br.
C. flava R.Br.
C. hirta Lindl.
C. huegelii Reichb. f.
C. latifolia R.Br.
C. menziesii R.Br.
C. reptans Lindl.
Calceana nigrita Lindl.
Diuris longifolia R.Br.
Elythranthera brunonis (Endl.) A. S. George.
Leporella fimbriata (Lindl.) A. S. George.
Lyperanthus nigricans R.Br.
Prasophyllum elatum R.Br.
Pterostylis nana R.Br.
P. recurva Benth.
P. vittata Lindl.
Thelymitra fuscolutea R.Br.
T. nuda R.Br.
Microtis unifolia (Forst. f.) Reichb. f.

Restionaceae

- Lyginia barbata* R.Br.
Loxocarya fasciculata (R.Br.) Benth.
L. flexuosa (R.Br.) Benth.
Hypolaena exsulca R.Br.
Restio nitens Nees.

Xanthorrhoeaceae

- Acanthocarpus preissii* Lehm.
Calectasea cyanea R.Br.
Dasypogon bromeliaefolius R.Br.
Lomandra caespitosa (Benth.) Ewart.
L. endlicheri (F. Muell.) Ewart.
L. micrantha (Lindl.) Ewart.
L. preissii (Endl.) Ewart.
L. suaveolens (Endl.) Ewart.
 L *L. sp.* (undescribed).
Xanthorrhoea preissii Endl.—Blackboy.

Ancient grooved stone axes from an alluvial terrace on Stonewall Creek, Kimberley, Western Australia

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Manuscript received 22 February 1977; accepted 22 February 1977

Abstract

Stone artifact assemblages probably relating to two successive stone industrial phases identified in other regional sites have been found at an alluvial terrace on Stonewall Creek, a tributary of the Ord River, Kimberley, Western Australia. Two of three grooved stone axes from the surface of a truncated soil at the terrace site are carbonate and iron encrusted, the source of the carbonate encrustations being an eroding younger soil unconformably overlying the truncated soil. The encrusted axes are older than a typical Ord valley late-phase stone artifact assemblage found on the surface of the younger soil. Correlations with similar grooved axes from Miriwun, a local rock shelter, and from Arnhem Land, where a similar two-phase stone industrial succession is known, suggest that the Stonewall Creek axes belong to the early Ord valley stone industrial phase, and are possibly early Holocene or late Pleistocene in age. Various data show that hunter-gatherer adaptation in the Ord valley may have been relatively stable since the late Pleistocene.

Introduction

In 1972, while engaged in a programme of archaeological salvage and survey, I recorded a number of archaeological sites on alluvial terraces in the Ord valley, Kimberley, Western Australia. This account describes the depositional sequence of stone artifact assemblages recovered from an alluvial terrace on Stonewall Creek, one of the tributaries of the Ord River and notes several significant artifacts from there. This site and its artifact assemblages have been briefly noted by Dortch (1977) and Mulvaney (1975, p. 194).

Stonewall Creek drains a 300 km² catchment area of barren ranges, rocky outcrops and semi-arid structural plateaus east of the Ord River (Fig. 1). This small stream system flows only during the summer wet season when the typically intensive rains often cause heavy flooding. During floods the system is capable of carrying relatively very large amounts of sediment, with the result that the shallow, braided middle reaches of Stonewall Creek are marked by massive alluvial terraces composed of gravel, sand and clay.

The Stonewall Creek terrace site

Numerous scatters of stone artifacts, presumably the remains of old campsites, occur on the surface of the terraces on Stonewall Creek. The largest and most important of these known at present is located on a weathered, partly eroded terrace situated within the fork

of Stonewall Creek and one of its tributaries 19 km east of the Ord River (16° 01' S, 128° 52' E; Fig. 1). The terrace, extending over 2 ha, has been used extensively as a campsite during the past, its chief attraction perhaps having been a series of semi-permanent pools in the granite bed of the main channel (Fig. 1). Much of the terrace is heavily eroded, and other parts have been badly damaged by gravel quarrying and other activities related to the construction of the adjacent paved road.

The alluvial terrace consists of two sedimentary units (Fig. 2). The upper or younger is a reddish sandy soil containing varying amounts of gravel; it unconformably overlies a light-coloured deposit which interfingers with thick pebble beds resting on the granite bedrock. This sequence of sediments ranges in thickness from 1-3 m, and always there is a clear interface between the reddish and light-coloured units. Two similar units extend in a terrace along the north bank of Stonewall Creek for several hundred metres downstream, and similar depositional sequences are exposed in other terraces several kilometres downstream. Gravel lenses occur within both units, and in one section there is a thick band of gravel separating the two units. There are also sections along the stream where the reddish sandy soil rests directly on the pebble bed above the bedrock. Thus the two units are not co-extensive and so are not components of a single soil profile.

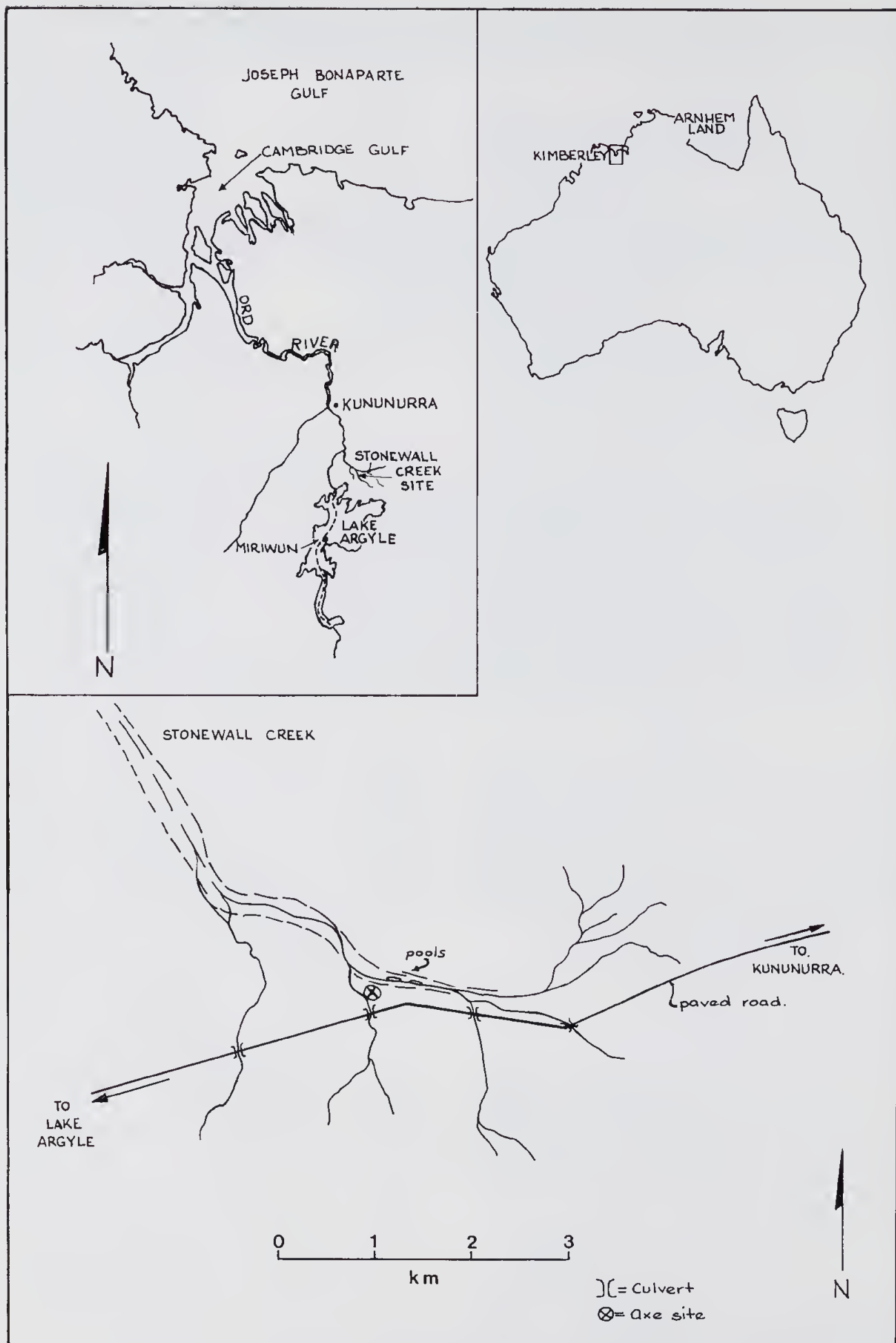


Figure 1.—The Stonewall Creek terrace site and the lower Ord valley, showing sites and localities mentioned in the text.

In all sections or horizontal exposures the light-coloured deposit has the appearance of a truncated soil. Using Stewart's classification of soils in the Ord-Victoria basin (Stewart 1970) the unit was tentatively identified as the subsoil of a lateritic podzol. Dr. G. A. Stewart, Land Resources Management, C.S.I.R.O., Canberra, has in part confirmed this identification, and suggests that it is the subsoil of a lateritic podzol of the Florina type or a meadow podzolic soil of the Marrakai type (G. A. Stewart, personal communication, 1973; Stewart 1970, p. 98). Both types of soils are poorly drained, decalcified, with ferruginous concretions or orange mottling throughout their profiles.

Preliminary first-hand examination of the light-coloured deposit shows that it is a pallid (yellowish-grey), cemented gritty clay with orange mottling; it is decalcified, weathered, and has a blocky columnar structure with cracks extending downward 30-70 cm (Fig. 2). Exposed horizontal surfaces contain numerous small ferruginous concretions, some clearly weathering out of the deposit. At one horizontal exposure, referred to below as the axe site, a small part of the surface, a few centimetres higher than the rest, has on it a 3 mm thick carbonate encrustation which is regarded as a remnant of a band of secondary carbonate derived from the weathering of the formerly overlying reddish sandy unit.

Stone artifact assemblages

The reddish sandy unit extends over most of the terrace within the fork of the two channels; it is completely removed in places leaving the surface of the underlying light-coloured deposit exposed over areas 50 to 1 000 m². The surface of the upper unit contains several hundred stone artifacts including numerous pointed blades of the leilira category, various kinds of invasively flaked points, some large (non-microlithic) backed points, some adze flakes and small flake-scrapers, a few flakes probably struck from discoidal or Levallois cores, a bifacially flaked edge-ground axe, denticulated and notched flakes, blades and bladelets, a number of core and pebble tools, and several grindstones or anvils, all of which typify the Ord valley late stone industrial phase (Dortch 1972; 1977).

This assemblage is concentrated on the northern and eastern parts of the terrace surface, where the reddish unit is largely uneroded, and on an adjacent, 600 m² deeply eroded exposure of the light-coloured deposit. A 30 cm² test pit dug into a partly eroded area of the reddish unit yielded two flakes about 10 cm below the surface and 20 cm above the lower unit.

None of the artifacts from the terrace shows signs of rolling or battering, and it is assumed that most if not all result from occupation of the terrace itself. Until now only one stone artifact has been collected from the stream bed

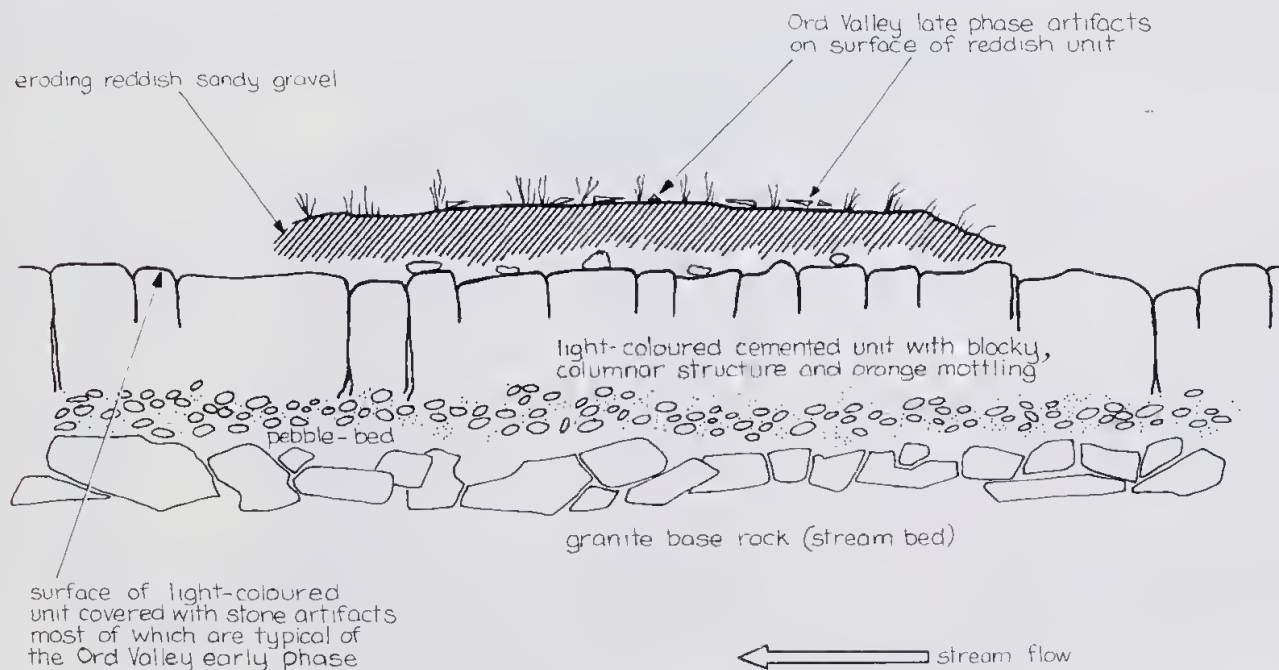


Figure 2.—Schematized view of the western edge of the axe site at the Stonewall Creek terrace site, Kimberley, Western Australia. The face of the reddish sandy unit is 50 m east of the lower unit's face.



Figure 3.—Axe B2212 from the Stonewall Creek terrace site.

immediately downstream from the terrace and none from the two channels forming the fork. However there are numbers of rolled artifacts in the stream bed a few kilometres downstream as well as in other stream channels in the Ord valley.

The main exposure of the underlying light-coloured deposit is at the terrace's western edge (Fig. 2). This is one of the most extensively eroded parts of the terrace, possibly because a large culvert a few metres upstream (Fig. 1) has the effect of confining and so increasing the velocity and scouring capacity of flood waters in the smaller channel. On the surface of this 1 000 m² exposure there are numerous weathered stone artifacts most of which are considered to be representative of the early Ord valley stone industrial phase (Dortch 1972; 1977; see discussion), a few points and blades typical of the later phase, and several tool forms common to both phases. Included are three pecked, ground and grooved axes, horsehoof cores and pebble tools, a number of thick flake-scrapers and notched flakes, and several grindstones and anvils. This assemblage is interpreted as a mixture of tools of different ages, though most of them, including the three axes, probably result from early-phase occupation at the site.

The three grooved axes were found within 60 m of one another on this exposure (i.e. the axe site, Figs. 1, 2). One of them (B2212; Fig. 3) was partly buried in what seemed to be superficially re-worked surface sediments from the light-coloured deposit. Another (B2213; Fig. 4) lay in a shallow gully cutting through the light-coloured deposit. Carbonate and iron encrustations on both faces of these two axes show that they have been buried within or beneath a weathering deposit. The third grooved axe (B2226; Fig. 5), an extremely weathered

specimen, was found on a gravel bed exposed in a heavily eroded part of the light-coloured deposit. A photograph of this axe *in situ* is seen in Mulvaney (1975, pl. 63).

Each of these axes has been partly shaped by pecking or hammer dressing though specimen B2212 seems to have been invasively flaked on one face (Fig. 3, left) before being pecked and ground. Bifacial grinding on specimens B2212 and B2226 (Fig. 5) extends from cutting edge to groove, whereas on specimen B2213 (Fig. 4) this is restricted to the cutting edge. The groove encircling each specimen has presumably been produced by pecking, or by a combination of pecking and abrasion. The very weathered condition of these axes prevents positive surface identification of the rock of which they are made. Mr. J. Clarke, Conservation Department, Western Australian Museum, has tentatively identified the stone of each specimen as gabbro or dolerite (J. Clarke, personal communication, 1976).

Since the light-coloured deposit is decalcified, the source of the carbonate encrustations on axes B2212 and B2213 is the younger unit, the reddish sandy soil. These two axes were either exposed on the truncated surface of the light-coloured deposit, prior to its burial by the reddish soil, or they were buried within this younger unit. The first alternative is more likely, since, as noted above, the surface on which they lay itself retains fragmentary remains of a secondary carbonate crust. No other artifacts from the terrace site are encrusted, and the only other encrusted artifacts presently known from the area are several weathered flakes, a pebble chopper and a possible upper grindstone from an exposure of a truncated soil several hundred metres downstream which is similar to the light-coloured deposit at the axe site.



Figure 4.—Axe B2213 from the Stonewall Creek terrace site.

It is clear that the two carbonate and iron encrusted axes are older than the stone artifacts from the surface of the reddish sandy soil, though they are not necessarily older than the soil itself. The two flakes excavated from within the reddish deposit could be younger than or much the same age as the two axes. None of the other artifacts from the various exposures of the light-coloured deposit at this terrace, including axe B2226 and other likely or probable early-phase artifacts from the axe site, can be unequivocally related to the artifact groups whose relative positions in the stratigraphical sequence is shown here.

The foregoing description of the stratigraphy of the terrace and its occupational sequence is firmly supported by this concise statement compiled by Dr. G. A. Stewart (personal communication, 1973).

"From its thickness, colour and texture the lower light coloured sandy clay with orange mottles appears to be a truncated profile of either Florina (lateritic podzolic) or Marrakai (meadow podzolic) soil. It would have been formed under prolonged water-logging, but with enough through drainage that all soluble materials such as calcium carbonate would have been leached from the profile. The calcium carbonate crusting on tools on the surface of the light coloured material must have been leached from younger overlying sediments from which the reddish sandy soil was formed."

Discussion

In the above, the grooved axes from the older unit, and the point and blade assemblages from both units of the Stonewall Creek terrace site are regarded as representing, respectively, the earlier and later Ord valley stone industrial phases. The interpretation of the Ord valley stone industrial sequence as having early and

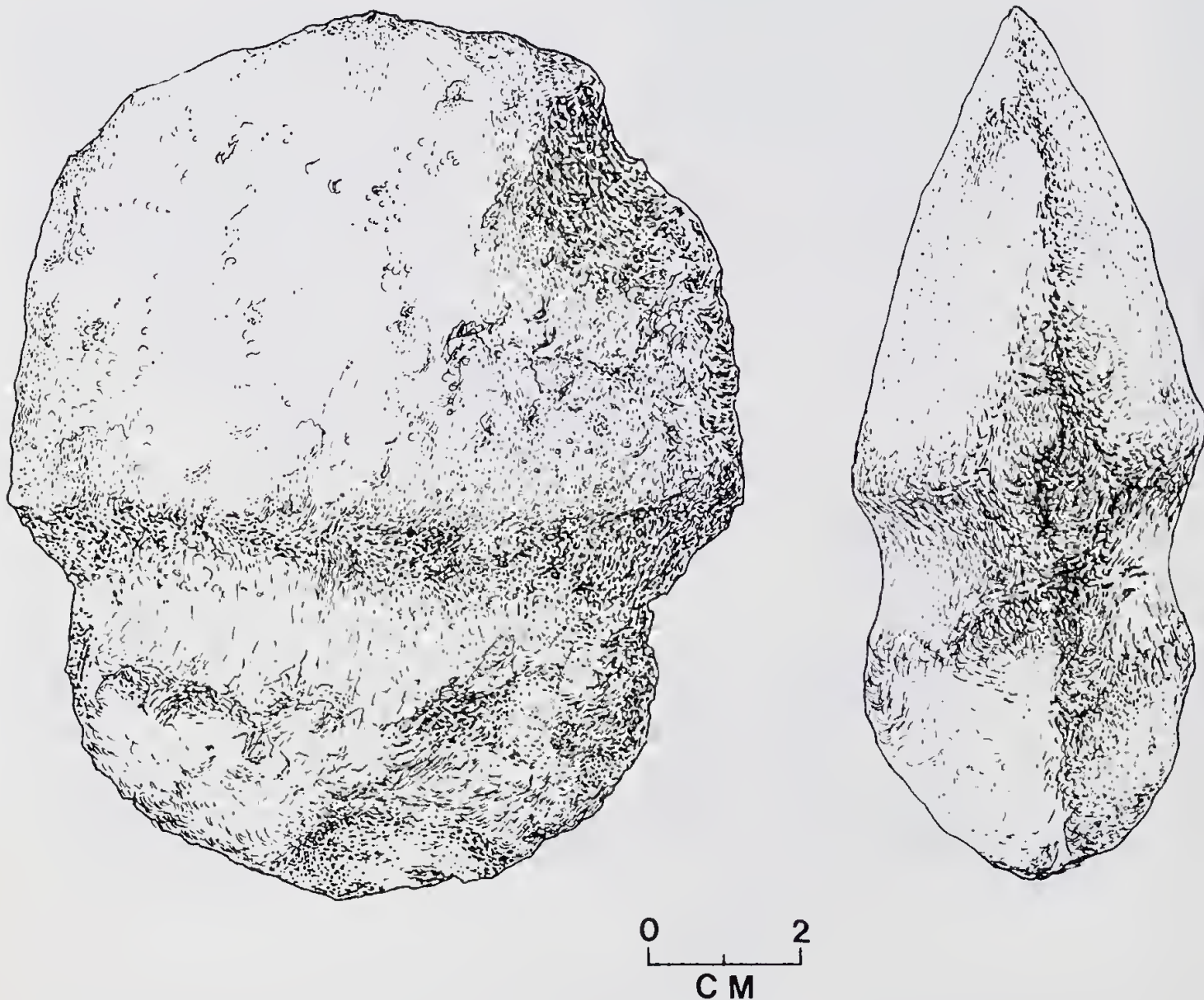


Figure 5.—Axe B2226 from the Stonewall Creek terrace site.

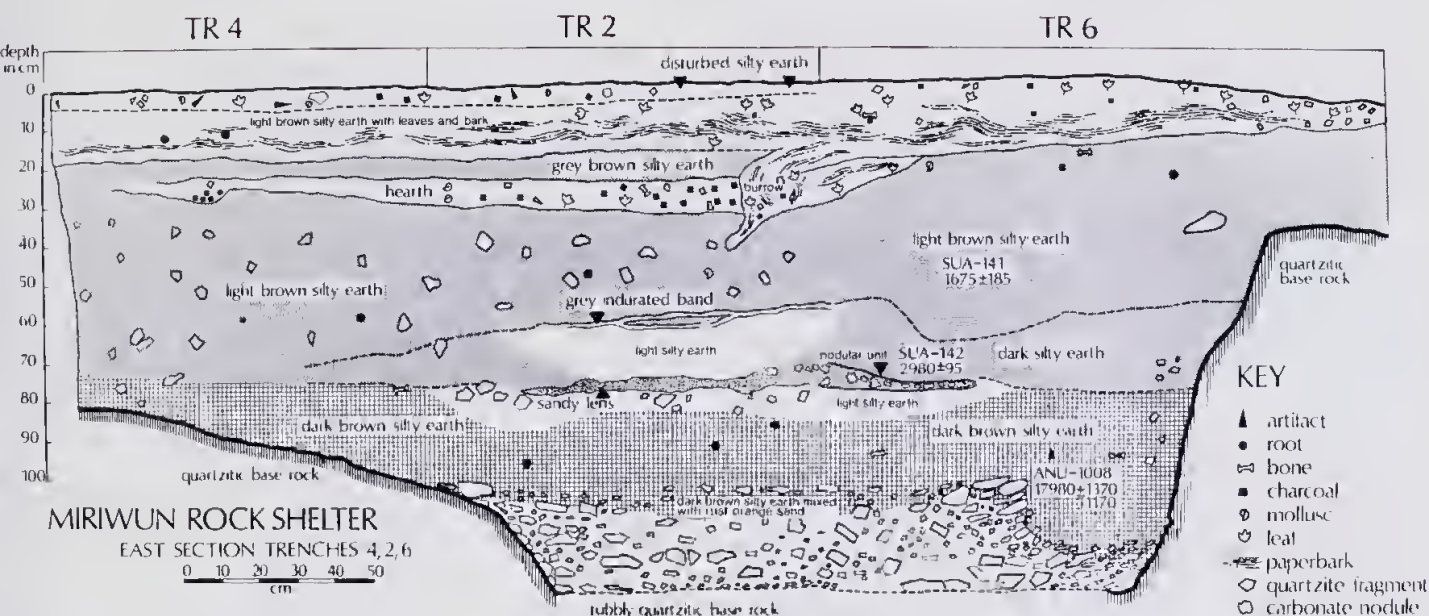


Figure 6.—East section of trenches 4, 2 and 6, Miriwun rock shelter, Lake Argyle, Kimberley, Western Australia. Approximate positions of radiocarbon dates mentioned in the text are shown.

late phases is very largely based on the succession of assemblages found in the stratified deposit at Miriwun rock shelter, a site 35 km SSW of Stonewall Creek which is now permanently inundated in Lake Argyle (Fig. 1; Dortch 1972; 1977).

The two lowermost layers (dark silty earth and dark brown silty earth) of the Miriwun deposit (Fig. 6) contain the definitive artifact assemblages of the Ord valley early stone industrial phase. These layers are overlain by several layers containing point, blade and flake tool assemblages typical of the Ord valley late phase, an industry identified at numerous open sites and rock shelters in the region. The later phase at Miriwun and other sites persisted until the modern era, and is part of the late-phase industrial complex which extends over the whole of Kimberley and western Arnhem Land (Dortch 1977). (For discussion of the distribution of stone points, adze flakes and other small flaked tools pertaining to this complex see Mulvaney 1975, p. 210-237.)

The upper of the two Miriwun early-phase layers (dark silty earth) is radiocarbon dated at 2980 ± 95 BP (SUA 142). This date is unexpectedly young and needs confirmation by others relating to terminal early-phase assemblages in this region. A charcoal sample from the lower layer at Miriwun containing an early-phase assemblage (dark brown silty earth) was radiocarbon dated at 17980 ± 1370 BP (ANU 1008). Thus early-phase occupation at the Miriwun site extended over a very long period, perhaps as much as 16 000 radiocarbon years.

It is significant to note that, aside from the Stonewall Creek specimens, the only other pecked, ground and grooved axe known from the Ord valley comes from the upper part of dark silty earth at Miriwun (Fig. 6), and so is dated

less than 3 000 BP (SUA 142). Also, from the lower part of the dark brown silty earth at Miriwun, dating to the late Pleistocene, there is a single flake with smoothing and striations on its dorsal face which has probably been struck from the face of a partly ground axe (Dortch 1977).

Stone axes are common features in Ord valley and other Kimberley late-phase assemblages. These axes are typically invasively flaked on both faces and only partly ground, and grooving is absent (cf. McCarthy 1967, fig. 30:11). Axes of this kind were being made by Ord valley Aborigines until a few decades ago, and older men of the Miriwung tribe, whose rightful lands extend over the area under discussion (cf. Tindale 1974, maps), are perfectly familiar with their technique of manufacture. I have shown the Stonewall Creek and Miriwun grooved axes to several Miriwung men, and they suggested that these are an earlier type.

The Ord valley grooved axes are typologically similar to the grooved axes associated with early-phase assemblages in Arnhem Land which are dated between about 6 500 and 25 000 BP (White 1967, 1971). It is probable that axes of this kind are also one of the characteristic components of the Ord valley early-phase stone industry, considering the provenances of the Stonewall Creek and Miriwun grooved axes, and the complete absence of such specimens in numerous Ord valley late-phase assemblages. The single flake with striated and smoothed surfaces from the dark brown silty earth at Miriwun also suggests that ground axes in the Ord valley date back to the late Pleistocene. However, tentative evidence for a grooved axe in a late-phase context in eastern Kimberley is provided by Tindale who found a site on Moolabulla Station 250 km south of Lake Argyle

where "... a Pirrian camping ground [presumably a point or late-phase assemblage] had in it a grooved pebble axe, while the overlying layer, representing the present time, had edge-ground axes..." (Tindale 1974, p. 85). The only other published report of Kimberley grooved axes seems to be in McCarthy (1967, p. 48).

The radiocarbon-dated faunal and stone industrial sequences at Miriwun show that early-phase economy there, dating back as far as the late Pleistocene, was similar to that recorded in this site's late-phase layers, the uppermost of which belong to the modern era (Dortch 1972, 1977). All these layers (Dortch 1977, fig. 4, tables 2, 3) contain the same range of animal foods, and the stone artifact assemblages in both phases include most of the same basic kinds of scraping, cutting, adzing, chopping and pounding tools. Several unequivocal grindstones are present in the late-phase assemblages, and a few probable fragments of lower grindstones and one definite upper grindstone occur in the early-phase assemblages. In short the most striking difference between the two phases is a very diverse and easily recognised range of small flaked tools (pointed blades, biface and uniface points, burins, etc.) present in the late-phase assemblages and absent in the early phase.

As noted elsewhere (Dortch 1977), Miriwun and the Stonewall Creek site can with some validity be interpreted as wet and dry season camps respectively. Hundreds of eggshell fragments of a summer-breeding water fowl, the pied goose (*Anseranas semipalmata*), throughout the Miriwun deposit show that the shelter was typically occupied during the summer wet season, though dry season occupation there cannot be discounted. Stonewall Creek, however, would often have been an uncomfortable or even unsafe campsite during the wet season, at least during past times when the stream regime was similar to that prevailing now. At present the stream system is notorious for sudden and violent flooding, and even after floods have subsided the terrace is sufficiently waterlogged and muddy to make camping unpleasant. On the other hand, during much of the dry season the

site is attractive because of its very reliable pools; these can not only contain water through most of the dry months (June to November), but also during the early part of the season provide surprisingly large amounts of fish. Admittedly the evidence supporting season of occupation at these two sites is in need of further development and testing. Nevertheless these data show that in this part of the Ord valley occupation and subsistence patterns are likely to have been stable for a long time, and that the marked change in the stone industrial succession which took place here a few thousand years ago is not necessarily indicative of significant shifts in land use or economy.

Acknowledgements.—The field research described in this paper was financed by the Australian Institute of Aboriginal Studies and the Western Australian Museum.

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Obituary

Desmond Andrew Herbert 1898-1976

It is with sadness that we record the death, at Brisbane on 8 September 1976, of Desmond Andrew Herbert, Emeritus Professor of Botany in the University of Queensland. Professor Herbert had a special interest for us in Western Australia as his first appointment after graduating B.Sc. at Melbourne University was to the position of Economic Botanist and Plant Pathologist to the State. After taking up his duties here early in 1918, in due course he became a foundation member of the Royal Society of Western Australia and served on some of its committees. He appreciated the importance of communicating to the State the results of his scientific researches, and he did this largely through the medium of the Journal of the Royal Society of Western Australia.

In retrospect it seems almost incredible the amount of botanical work Herbert published in the relatively short period that he was Economic Botanist here. Despite his comparative youth (I believe he was not yet 20 when he was appointed) his work has the stamp of scientific maturity, and his paper dealing with the structure and parasitism of the Christmas Tree (*Nuytsia floribunda*), read to the Society in April 1919, is a classic. His interest in the problem was aroused when, in his capacity as Plant Pathologist, he investigated the matter of a field of carrots in Como which were starting to die off when only half grown. He found white collar-like structures strangling the carrot roots and traced the connections of these back to a clump of *Nuytsia* trees 40 m away. He then began a careful study of the Christmas Tree and demonstrated that it could parasitise the roots of many other plants. His work ended, once and for all, the long-standing botanical controversy as to whether *Nuytsia* was or was not parasitic, and vindicated the theoretical views of Harvey. His anatomical studies of the plant also led to an understanding of its curious growth habit. His work on the parasitism of the Sandalwood (carried out jointly with C. A. Gardner, whose interest in botany he had aroused and fostered) followed. Believing that it was essential to have a continuing record of new plants discovered and described, Herbert next inaugurated a series of papers called "Contributions to the Flora of W.A." and up to the end of 1921 four papers had been published. However, these three exciting discovery years were all that

Herbert was to spend in Western Australia as he accepted an invitation to the Chair of Botany in Manila.

It has been pointed out elsewhere (Presidential Address, 1971) that the measure of the potential importance for Western Australia of botanists like Herbert, had they stayed longer, is indicated by the quality of their later work. It may be appropriate, therefore, to briefly outline Des Herbert's contribution to botany in Queensland, where he joined the University in 1924 and became the foundation Professor of Botany in 1948. His interests now lay more in ecology and plant geography, and in 1935 he devoted his presidential address to the Royal Society of Queensland to an account of the relationships of the Queensland flora. In the same year his presidential address to Section M of ANZAAS dealt with the question of the climatic sifting of Australian vegetation. Being again President of Section M in 1960 (a rare honour) he reported on the tropical and sub-tropical rain forests of Australia. Despite the demands of teaching and administration (he was twice dean of the faculty of science in the University and for many years the local secretary for ANZAAS in Brisbane), Professor Herbert published over 40 significant scientific papers and also wrote the highly successful horticultural work entitled "Gardening in warm climates".

It was through ANZAAS that I first met Des Herbert in Perth in 1947 not long after I had arrived here myself. I found him to be a stimulating personality, and he had an extraordinarily good knowledge of the vegetation of Western Australia although he had been out of the State for many years. I saw him frequently after that at various meetings and profited much from discussions with him.

Professor Herbert retired in 1965 and in 1966 he was awarded the C.M.G. for his services to botany. It can truly be said that the foundations for these services were laid during his time in Western Australia and were, in part, expressed through the medium of our Journal. His continuing interest in the scientific work going on in this State is reflected in the fact that over the years he retained his membership of the Society. In 1964 Council honoured him by electing him to Honorary Membership.

B.J.G.

A sedimentological study of Devil's Lair, Western Australia

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Manuscript received 22 February 1977; accepted 22 March 1977

Abstract

The sediments in Devil's Lair cave, Western Australia, show a complex sequence of depositional and diagenetic events. Most of the clastic sediments are derived from weathered aeolianite. The main feature of the cave sediments is their textural uniformity, seemingly independent of microclimatic variations; this is inherited from the aeolianite source rock. The clastic sediments are interbedded with complex flowstone layers, formed during sedimentation pauses related to changes of the cave entrance, and are lithified through carbonate cementation. Human or animal activity had little influence on either the composition or the diagenesis of the cave sediments.

Introduction

Devil's Lair is a small cave about 5 km from the sea in Quaternary aeolianite in the Cape Leeuwin-Cape Naturaliste region of the extreme southwest of Australia (Fig. 1). The cave deposits have recently been excavated by members of the staff of the Western Australian Museum, leading to a series of important archaeological and biotic finds which are summarised in the works of Dortch (1974), Dortch and Merrilees (1972, 1973), and Baynes, Merrilees and Porter (1976). The writer studied samples from the 1970 excavations and collected further samples during a visit in April 1974.

General setting

Geology

Devil's Lair cave was formed in the calcareous aeolianite (Tamala Eolianite) capping the Precambrian crystalline rocks that form the Leeuwin-Naturaliste ridge. The mostly lithified dune deposits occur at elevations of up to 230 m, and their distribution is shown in Fig. 1. Although the aeolianite is predominantly a limestone, the calcium carbonate content ranges from 10% to 90%. The calcareous particles consist of sponge spicules, fragments of mollusc shells, calcareous algae and foraminifera. The remainder of the rock consists of quartz, feldspar and heavy minerals. The older dune deposits are cemented by calcium carbonate. Caves are developed in the lithified dunes and these are generally found on the leeward side of the ridge, possibly formed by solution processes acting below the water table (Bastian 1964). The cave systems are complex and interconnecting, and many open out of dolines, as in the case of Devil's Lair and Nannup Cave, which open from the same doline.

Soils

The soil pattern of the coastal dunes varies with erratic and variable segregation within the parent material as a result of leaching, the dominant pedogenetic process. They generally have a superficial layer of dark brown loamy sand, containing some organic matter and sel-

dom more than 6 cm thick, which overlies 6-42 cm of dark brown sand with a little clay, and a further 6 cm of brown sand over the

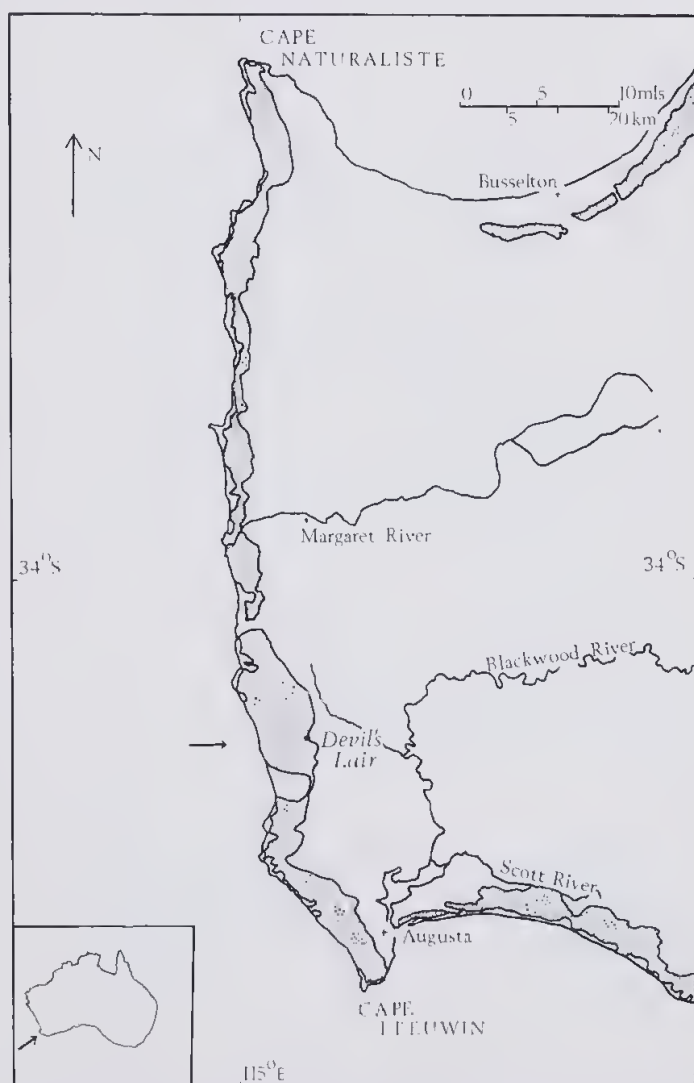


Figure 1.—The Cape Leeuwin-Cape Naturaliste region of Western Australia, showing the location of Devil's Lair. The shaded area represents the approximate distribution of the Tamala Eolianite. Modified from Lowry (1967).

limestone cap rock. Lumps, nodules and bands of ferruginous material are common, and such soils present a marked contrast to the acid podsols which develop further inland.

Climate and vegetation

At present the vicinity of the cave has a high annual rainfall of 910–1 520 mm, falling in the winter months, and the vegetation is an open Karri forest (*Eucalyptus diversicolor*) with an understorey including Peppermint (*Agonis flexuosa*). Low woodland, scrub and open heath occur nearer to the coast.

Cave morphology

The cave consists of a single chamber, irregular in shape, with two separate entrances, one of which (the northern) is now blocked by a talus cone composed of clastic deposits and flowstone (see Fig. 2). The southern entrance

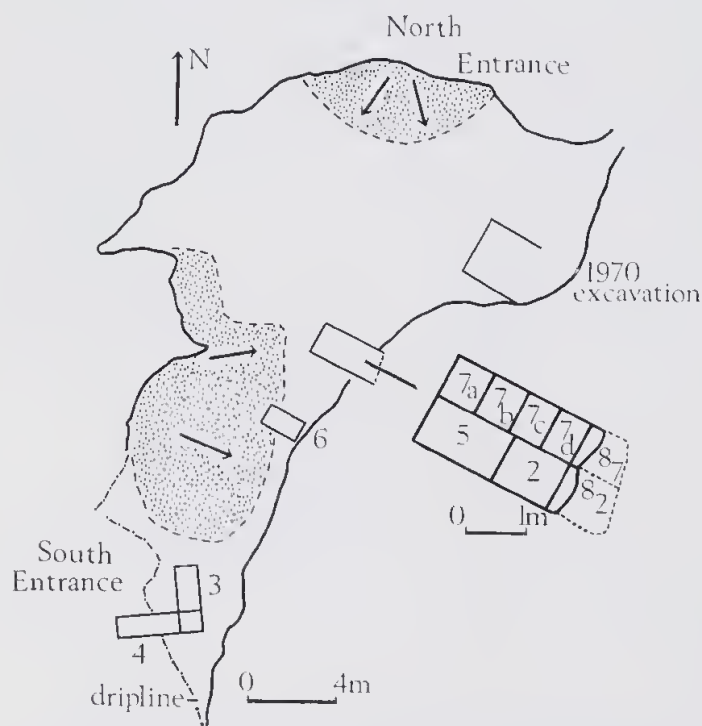


Figure 2.—Sketch plan of the cave floor of Devil's Lair, showing the location of excavation trenches. The shaded areas indicate the approximate extent of the main talus cones.

is the present means of access, but the slope of the strata suggests that it was not open during most of the depositional history of the cave, and that the greater part of the sediments entered from the north.

The floor of the cave is mainly covered by a sheet of flowstone of irregular thickness. Active speleothem formation continues and water still enters the cave through crevices. Cave temperature remains relatively constant and light penetrates into the cave, with the exception of the extreme rear (northern area), more than 15 m from the present entrance.

Clastic sediments

The sediments consist of interbedded sand, flowstone and stalagmite, together with lithified bands and occupation horizons. In places they have been disturbed by animal activity, and the occasional occupation by human groups is evidenced by the presence of hearths and pits. Nonclastic material includes bone, artifacts, charcoal and other biotic remains. The maximum thickness of the sediments is in excess of the 4 m established in the excavation. A radiocarbon date from immediately below the uppermost flowstone which seals the deposits indicates the end of clastic sedimentation shortly before 6490 ± 145 BP. The oldest samples are probably older than 30 000 BP.

Analytical procedures

Trenches 2, 5, 7 a-d, 8 (2) and 8 (7) (Fig 2) were sampled in 1974 for laboratory analysis, together with samples from Trench A1 which were collected in 1971. Dry sieve analysis, grain surface texture studies and determination of chemical composition were carried out in the laboratory (Shackley 1975) to complement the field data. Field observations focussed on description of composition, colour, texture, cementation and compaction. Field tests for pH, phosphates and humus were also carried out.

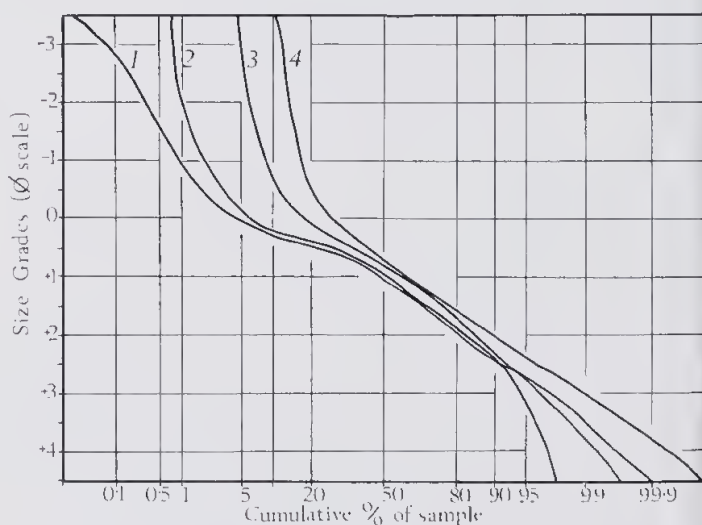


Figure 3.—Particle size distribution curves, plotted on arithmetic probability paper, for samples from Devil's Lair. 1—Low orange brown earthy layer, Trench 6. 2—Middle orange brown earthy layer, Trench 6. 3—High orange brown earthy layer, Trench 6. 4—Trench 6, top first orange brown earthy layer.

Composition

Thirty samples of the clastic sediments, taken from different trenches, were subjected, after decalcification, to a detailed particle size analysis by dry sieving. Table 1 shows that the sediments consist chiefly of rather poorly-sorted gravelly quartz sands, generally positively skewed and leptokurtic. The proportion of mud (silt and clay) in the samples was very low, only 4 samples containing more than 5%. Fourteen

Table 1.
Particle size analysis, Devil's Lair sediments.

Source of Sample	Approx. depth (cm. below cave datum)	Weight pro- cessed (g)	Composition			Descriptive Parameters				Textural Description (Folk 1954)
			Gravel (%)	Sand (%)	Mud (%)	Mean (ϕ)	Stand- ard Devi- ation	Skew- ness	Kurt- osis	
Topsoil outside cave	(above)	878.2	20.5	73.4	5.9	0.69	2.00	0.29	1.06	Gravelly sand, moderately sorted, mesokurtic
Tr. 7c, 'Dark earthy layer'	75	1 645.0	13.7	85.4	0.7	0.78	1.42	-0.18	1.62	Gravelly sand, poorly sorted, very leptokurtic
Tr. 5, 'dark earthy layer'	60	845.0	3.9	89.9	6.1	1.35	1.48	0.32	1.17	Gravelly sand, moderately sorted, mesokurtic
Tr. 5 'earthy' band in 'flow- stone complex'	80	1 230.0	3.7	95.6	0.5	1.07	1.04	-0.29	0.99	Slightly gravelly sand, poorly sorted, mesokurtic
Tr. 5, 'first orange brown earthy layer'	150	1 289.0	0.4	99.4	0.0	1.13	0.97	0.36	0.84	Slightly gravelly sand, moderately poorly sorted, platykurtic
Tr. 5, 'light earthy layer'	220	1 108.0	6.4	92.8	0.7	0.78	1.01	0.03	1.66	Gravelly sand, poorly sorted, mesokurtic
Tr. 5, 'second orange brown earthy layer'	240	1 087.0	1.1	97.9	0.9	1.10	0.90	0.35	0.99	Slightly gravelly sand, moderately poorly sorted, mesokurtic
Tr. 6, stratigraphic position uncertain	?	458.0	13.1	80.1	6.7	1.09	1.69	0.23	1.18	Gravelly sand, moderately sorted, mesokurtic
Tr. 6, stratigraphic position uncertain	?	1 197.0	4.3	95.4	0.2	0.99	0.99	0.27	0.94	Slightly gravelly sand, moderately poorly sorted, mesokurtic
Tr. 6 cave pearl and bone layer	110	487.0	53.3	45.9	0.6	-0.84	2.14	0.24	0.78	Sandy gravel, very poorly sorted, platykurtic
Tr. 6, Hearth 1	120	390.0	6.1	91.0	2.8	1.13	2.27	0.18	1.33	Gravelly sand, poorly sorted, leptokurtic
Tr. 6, 'brownish earthy layer'	150	1 615.0	0.8	98.7	0.3	1.12	0.90	0.32	0.86	Slightly gravelly sand, moderately poorly sorted, platykurtic
Tr. 6, 'brownish earthy layer'	200	2 225.0	1.9	94.9	3.1	1.06	0.91	0.20	1.25	Slightly gravelly sand, moderately poorly sorted, leptokurtic
Tr. 6, 'brownish earthy layer'	250	1 427.0	9.6	89.8	0.5	0.95	1.49	0.15	1.69	Gravelly sand, poorly sorted, leptokurtic
Tr. 8? Hearth 2?	?	1 423.0	17.2	82.6	0.0	0.34	1.44	-0.41	1.45	Gravelly sand, poorly sorted, very leptokurtic
Tr. A1, Grey 'Ashy' lens	105	501.0	26.0	73.7	0.1	0.38	1.65	0.30	0.66	Gravelly sand, poorly sorted, platykurtic
Tr. A 1, 'rubbly layer'	110	221.2	39.9	57.7	2.3	0.15	1.67	-0.12	0.68	Sandy gravel, poorly sorted, platykurtic
Tr. A 1, 'earthy layer'	130	1 216.0	3.3	94.7	1.8	1.03	0.94	0.21	1.14	Slightly gravelly sand, moderately sorted, leptokurtic
Tr. A 1, 'rubbly layer'	152	1 396.0	2.7	94.5	2.6	1.18	1.07	0.15	1.18	Slightly gravelly sand, moderately poorly sorted, leptokurtic
Tr. A 1 'earthy layer'	170	1 245.6	8.1	89.7	2.1	1.10	1.29	0.10	1.63	Gravelly sand, poorly sorted, leptokurtic
Tr. A 1, 'rubbly layer'	230	1 504.2	19.8	79.6	0.5	0.21	1.58	0.01	1.07	Gravelly sand, poorly sorted, mesokurtic
Tr. A 1, 'thin flowstone'	234	707.3	1.6	94.0	4.2	1.12	1.16	0.27	1.40	Slightly gravelly sand, poorly sorted, leptokurtic
Tr. A 1, 'earthy layer'	235	252.3	17.5	79.1	3.2	0.57	1.77	0.09	1.43	Gravelly sand, moderately poorly sorted, leptokurtic
Tr. A 1, 'dark earthy layer'	250	1 178.7	4.7	94.5	0.7	1.02	1.08	0.09	1.39	Slightly gravelly sand, moderately poorly sorted, leptokurtic
Tr. A 1, 'light sandy layer'	264	2 797.4	15.8	76.0	8.1	1.44	2.03	0.14	1.03	Gravelly sand, moderately sorted, mesokurtic
Tr. A 1, 'earthy layer with thin sheets of flowstone'	280	851.4	4.8	84.3	0.8	0.78	1.54	0.26	0.87	Gravelly sand, poorly sorted, platykurtic
Tr. A 1, 'banded earthy layer'	288	1 610.6	1.3	97.3	1.2	0.90	0.80	0.39	1.60	Slightly gravelly sand, moderately sorted, very leptokurtic
Tr. A 1, 'banded earthy layer'	300	1 023.4	3.7	94.1	2.1	1.14	1.06	1.25	1.13	Slightly gravelly sand, poorly sorted, leptokurtic
Tr. A 1, stratigraphic position uncertain	?	1 465.6	19.3	79.1	1.4	0.17	1.53	0.03	1.40	Gravelly sand, poorly sorted, leptokurtic

samples contained more than 90% and 26 samples more than 75% sand, but only 1 sample had more than 50% gravel. Some particle size distribution curves (Fig. 3) illustrate the uni-modal nature of the sediments, the bulk of which consist of particles of grain sizes 0.5-1.5 ϕ (coarse/medium sand). The Inclusive Graphic Statistics of Folk and Ward (1957) were calculated for each sample using the computer program SIEVETTE (Shackley 1975) and are also listed in Table 1. They show the mean grain size of the sediments to be 1.17 ϕ (medium sand), and that the skewness values tend on the whole to be positive. However, the existence of 4 samples with negative skewness values is interesting, since this feature has been taken by many workers (for example Friedman 1961) as typical of beach sands.

The most important result of this analysis is to emphasise the striking uniformity of the deposits, which are composed of sand of very similar textural composition. This is an unusual feature of cave deposits which, since they are formed under rather complex sedimentological conditions, tend towards greater variety. It seems unlikely that the results of this analysis can be of any value in detecting definite trends, or in defining stratigraphic horizons. Minor textural differences are principally attributable to variations in the amount of coarser clastic particles weathered from the cave walls, and to later disturbance, and no palaeoenvironmental evidence of value can be deduced from these results. The sediments are mostly consolidated and the baulks of the trenches need no supports. Thin section study combined with treatment by hydrochloric acid showed that this consolidation was due to a calcite cement.

Origin

The cave sediments could either be derived from weathering of the aeolianite inside the cave or from material weathered outside the cave and redeposited. In either case the primary source is the aeolianite but the weathering products have been mixed with organic matter and humus from exterior topsoil, together with the debris of human and animal occupation. The source material controls to a large extent the nature of the weathering products, and in this case the cave sediments directly reflect the composition of the aeolianite.

The cave deposits have been subjected to some degree of diagenesis, including the formation of speleothems and gypsum. Their characteristics therefore depend on the textural and mineralogical characteristics of the lithified dune and beach sands, subsequent weathering, transport, and renewed diagenesis. These features and processes are related to climate, but the nature of the resulting sediments suggests that it was not the controlling factor, a situation quite contrary to that generally found in European caves.

The stages in the formation of the deposit are shown diagrammatically in Fig. 4. The sediments in question bear many relict features

from previous stages in the cycle, for example the negative skewness values of some layers of sediment, which seem likely to be related to the original composition of aeolianite.

At present the primary sedimentological process operating within the cave is the deposition of calcium carbonate as a cementing agent, but very little active weathering occurs. It is therefore difficult to envisage the production of the deposit *in situ* as the exclusive product of weathering under a different climatic regime. It also seems unlikely that local macroclimate greatly influences the microclimate of the cave, certainly not enough to produce this type and depth of deposit.

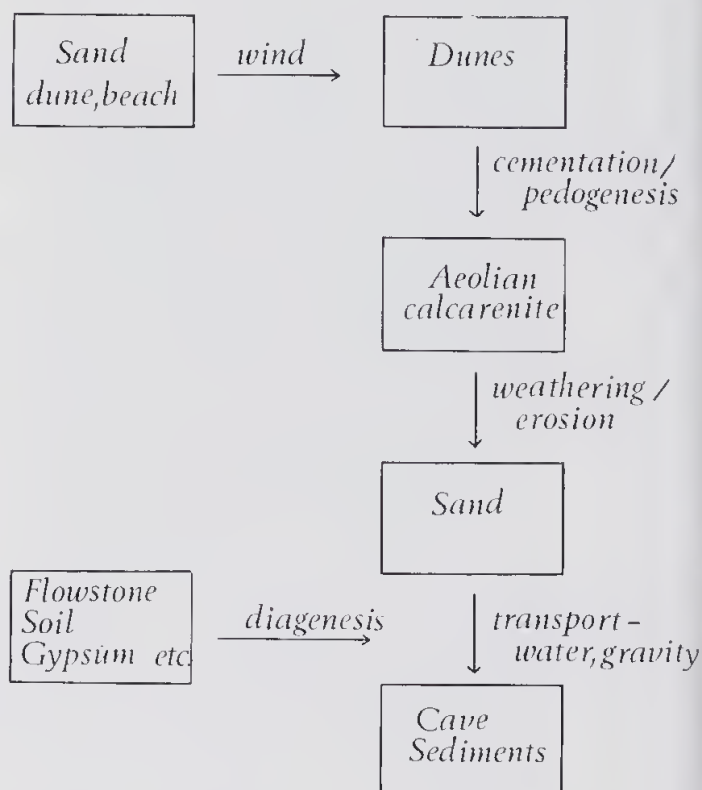


Figure 4.—Flow diagram indicating the processes which have contributed to the formation of the Devil's Lair sediments.

This suggests that the deposits were derived from material weathered from the aeolianite *outside* the cave, and redeposited inside, via the north entrance. The nature of the material and of the cave entrance suggest that wind was not the transporting medium, and it is suggested that the material either arrived in water-transported 'bursts', as suggested by Dortch and Merrilees (1973) as a result of especially heavy rainfall, or that it arrived as a continuous slow trickle.

If sediment had accumulated on the surface during the dry season and was then washed into the cave during the rainy season, one would expect more systematic laminations and a greater variation in the nature of the sediments. Laminae were, however, more obvious in Trench 9 (nearer the cave wall) than in

Trench 5, at the same stratigraphic levels. However, the lack of more extensive laminae does not necessarily negate the 'burst' sedimentation theory, since there seems to be no sedimentological process which could produce such a very slow rate of accumulation, less than 1 mm per year, if it were continuous.

An examination of the surface textures of the cave sediments shows them to be identical to those of the aeolianite, although showing evidence of many different sedimentological processes, and there seems to be no doubt that this was the source material. The composition of the topmost ('dark earthy') layer is rather different, and it has a high clay and humus content, which suggests that it was primarily derived from topsoil, washed into the cave from the south entrance after the north entrance became sealed by the talus cone.

The very slow rate of accumulation is indeed remarkable, and was commented on by Lundelius (1960) as well as by later workers. Dortch and Merrilees (1972) consider that the rapid burial of a prominent stalagmite indicates a fast rate of deposition for the upper part of the deposit, and they suggest that accumulation of sediment in the cave was not slow, but intermittent. The writer agrees with this.

A series of samples taken from depths of 320, 250 and 200 cm below cave datum in Trench 8₂ which would span the maximum cold of the last glaciation (the period 23 000-16 000 BP) show no appreciable variations. If the variations in the sedimentation pattern of the cave had been attributable to climatic fluctuations then it would be expected that these samples would show considerable differences. Analysis showed them to be similar in colour, phosphate and humus content, as well as in particle size. No variation in grain surface texture could be observed under the microscope and the conclusion was drawn that either there had been no major climatic change or that the cave sedimentation was independent of macroclimate. The period covered by these samples would be included in the major recorded fall in sea level between 40 000-15 000 BP, but it has been suggested that local climate did not change drastically during this period. However, it would seem that climate had little influence over the sedimentation pattern, unless increased rainfall at any period stimulated more sedimentation 'bursts'. This might well have happened in the upper part of the deposits.

A study of the faunal changes in Devil's Lair (Baynes, Merrilees and Porter 1976) suggests the possibility of an alteration in the position of the forest zone near Devil's Lair, perhaps related to a glacioeustatic rise in sea level. It seems probable that some time after 19 000 BP the sea west of the cave fell at least 100 m below its present level, and then began to rise again, reaching a level of -40 m by 12 000 BP and its present level some time during the post-glacial (Baynes, Merrilees and Porter 1976). It is clear then that the deposition of the 'first orange brown earthy layer', bounded by a radio-carbon date of 19 000 BP at the base and 12 000

BP at the top, must have taken place during a period of marked palaeoenvironmental change. Bearing in mind that at some time during this period the sea would have been as much as 20 km further away from the site than at present, and that climate, weathering and erosional processes must inevitably have fluctuated, one can say that the uniformity of the deposits must indicate independence of climatic control.

Flowstone horizons

Composition

Two distinct varieties of speleothems are present in Devil's Lair, discrete stratified flowstone layers occurring approximately parallel to the surface of the floor on which they are formed, and secondary calcitic penetration of the clastic sediments. In addition to these forms, individual stalagmites occur, such as the one figured by Dortch and Merrilees (1972). Many of the flowstone layers in the cave are rather thin, of the order of 1 cm in thickness. The flowstone levels seem often to be associated with quantities of charcoal, sometimes included within them and sometimes occurring as charcoal rich bands immediately underneath. Although the flowstones consist mainly of calcite precipitate they may also contain quantities of clastic deposits, but there are sharp boundaries with the overlying clastic layers; they are composed of large (> 0.02 mm) clear, elongated crystals whose long axes occur perpendicular to the precipitating surface.

Formation

Calcitic flowstones are formed by the precipitation of calcite from thin films of water. However, only a small quantity of water is required and this can be met with under a variety of climatic conditions. There is no close relationship between flowstone formation and climatic control, although it is a common assumption that the deposition of flowstone layers represents a wet episode should a large quantity of water be required. Two main factors seem to control the formation of flowstone layers, the most important being the rate and continuity of clastic sedimentation, and secondly, and to a lesser extent, fluctuations in surface climate which produce changes in vegetation and thus changes in the amount of carbon dioxide which is dissolved in the groundwater.

Frank (1973) noted that the rates of clastic alluviation in caves, particularly in entrance facies, far exceed the precipitation rate of calcite, and may even be deposited 7 times as fast as stalagmite could possibly accumulate. This is important for Devil's Lair, where it is suggested that the majority of the clastic material entered the cave very fast indeed, as 'bursts', which were intermittent and resulted in an overall slow rate of sedimentation. Thus it would clearly have been impossible for flowstones to have developed during a sedimentation 'burst', irrespective of the amount of ground water available.

Kukla and Lozek (1958), working on similar problems, concluded that the presence of flowstones in a clastic sequence indicated a slowing down or a complete cessation of clastic deposition. It is therefore clear that whatever the climatic fluctuations the flowstone layers within the cave mark periods of pauses in sedimentation, and must also mark periods when the cave was not being utilised either by animal or human groups, since this would have necessitated an open entrance which would have permitted sediment accretion. It is unlikely that extensive deposits of flowstone could have formed while the entrance was open. This does not preclude the inclusion of biotic or archaeological remains within the flowstone, since as flowstone deposition was rather slow it is inevitable that even the action of gravity would result in some debris becoming incorporated into the layers, or flowstone would accumulate round objects protruding from the general surface.

Butzer (1971) stated that a sub-humid moisture regime and a temperate climate is optimum for speleothem formation. Corbel (1952, 1959, 1961) estimated that when the mean annual temperature is greater than 18°C and the mean annual rainfall exceeds 1000 mm speleothems would form in all parts of a cave. The present climate around Devil's Lair is far milder than these limits, but the cave interior is still rather damp, with calcareous solutions dripping inside the cave during the wetter months. Speleothem formation is still continuing at the present day, although not resulting in continuous flowstone layers.

It is possible (Baynes, Merrilees and Porter, 1976) that both temperature and quantity of rainfall may have increased between 19000 and 12000 BP, and that this may have had some effect on the deposition of the upper flowstones. However, the solution and precipitation of calcite is not only dependent on temperature and rainfall, but is also a function of the availability of carbon dioxide, so that the control is indirect since it is the surface vegetation and soil micro-organisms which control carbon dioxide availability. Schmid (1958, 1963) and Kukla (1961) maintain that speleothem growth is enhanced by warm humid climates where there are substantial amounts of surface vegetation to provide the carbon dioxide for the solution of calcite, and then enable calcite-laden water to precipitate the mineral after entering the cave.

Frank (1973), in a study of flowstone layers in Australian caves, stresses the relationship between cessation of clastic deposition and the formation of flowstone, and the fact that the latter is not climate-dependent. It seems reasonable to regard the flowstone layers in Devil's Lair as marking sedimentation pauses, probably resulting from the temporary blocking of the cave entrances, rather than as intervals of warmer, wetter climatic conditions. However, bearing in mind the conclusions of Gams (1968), working on the Postojna cave, which provided additional support for the theory that a surface environment of high precipitation and

dense vegetation is optimum for encouraging speleothems, it is worth considering in the case of Devil's Lair that an increase in local vegetation cover might be a contributory factor in flowstone formation, especially in the thick flowstone at the top of the deposit. This layer, visible for example at the top of the west face of Trench 5 (Dortch and Merrilees 1973, Fig. 5) was clearly deposited after 12000 BP, before the deposition of the 'dark earthy' layer, 325 ± 85 BP, which originated through a different set of processes and via a different cave entrance. It seems likely that the processes responsible for the deposition of the main bulk of the clastic sediments became inoperative around 12000 BP and that the sedimentation pattern of the cave was interrupted. After this time the thick band of flowstone was deposited and sedimentation then resumed, resulting in the 'dark earthy' layer which has a high humus content and seems largely to consist of redeposited topsoil. The depositional hiatus marked by this thick and very complex multiple flowstone was almost certainly caused by the blocking of the north entrance.

Diagenesis

The clastic cave sediments are characterised by their mostly inherited features which reflect previous depositional environments. Transport into the cave has had little influence on the sediments, but diagenesis, which to some extent reflects climate, has left some imprint. Diagenetic processes include lithification through carbonate cementation, the formation of gypsum deposits, movement of soil phosphates, humus and soluble salts, in addition to biogenic disturbance through, for instance, penetration of rootlets and human activity.

Human and animal activity

Human activity is evidenced principally by the disturbance of the deposits, for example by digging of pits and the remains of hearths, and by the addition of archaeological material, either artifacts or food debris.

Human groups entering the cave have also resulted in the addition of phosphates together with increments of humus and plant material from outside. Animal activity has proceeded along similar lines, again resulting in disturbance and also in waste breakdown products such as colophane.

Several lenses have been recognised as hearths on the basis of increased charcoal content and the presence of burnt bone. Examination of such hearth deposits under the microscope showed that the quartz sand grains were heavily coated with smaller particles, giving them a 'dusty' appearance, and that many agglomerations of cracked and burnt grains occurred. Modifications of grain surface texture included mazes of fine cracks, angular splitting and encrustations of charcoal. These microscopic characteristics reinforce the interpretation of hearths.

Lithification

The process of lithification of the sediments by the addition of calcitic cement is certainly the most important diagenetic process operating. This must be carefully distinguished from the formation of flowstone, since the calcite precipitation here occurs after the deposition of the clastics, the grains are smaller, crystal formations unclear and there are no defined boundaries between calcite cement and clastic grain. The cohesion imparted by this process has already been discussed. All the Devil's Lair deposits have been affected to some degree, and in some cases this has resulted in lithification. The chemical processes are, however, similar to those active in the formation of flowstone, namely the precipitation of calcite from solutions rich in carbon dioxide, but this occurs after the deposition of the clastics and is a continuing process.

Formation of gypsum

Minor deposits of gypsum are found within the deposits, frequently associated with rootlets and occurring in larger concentrations around roots and root holes. The finest rootlets are often completely coated in white gypsum, and occasionally moulds are left where roots have once been. Under normal weathering any sulphide present in bedrock is oxidised to sulphate, and in the course of soil formation the sulphate becomes available to plants and micro-organisms, and part of it is leached. Under temperate conditions and in well drained soils, the sulphur is present in organic matter, probably in amino acids such as cystine and cysteine, but most is removed by leaching. Under more arid conditions it is retained and often separates out as gypsum deposits. Oxidation of sulphides present in organic matter and plants is catalysed by the action of bacteria which make use of the energy released. Leaching is not an important process within these cave sediments. The gypsum deposits appear to have formed around the roots by the processes described above, and the movement of water within the cave sediment is not sufficient to disperse them.

Conclusions

In any study of this type it is important to relate the deposits to the morphology and bed rock of the cave, and in this case the latter is of paramount importance. The aeolianite in which the cave is developed has governed the formation and constituents of the sediments, and any other factors including climatic variations, human or animal activity, being of only secondary importance. The sequence of deposits is interesting because of extreme textural uniformity, seemingly independent of macroclimatic influences. The primary source of the cave sediments is undoubtedly weathering of the aeolianite, additional material being washed and blown in from outside, or brought in by animals or human groups visiting the cave. Flowstone formations, which constitute a substantial part of the sequence and are interleaved with the clastic sediments, are related to pauses in clastic sedimentation caused by blocking of the cave

entrances. The cohesion of the deposits is effected by secondary accretion of calcium carbonate around the quartz sand grains, forming a cement. The deposits retain many of the features of previous stages in the depositional cycle, a situation completely contrary to that found in any of the limestone caves of the northern hemisphere. It is suggested that the sediments accumulated in intermittent bursts, perhaps related to episodes of increased rainfall.

Acknowledgements.—The writer gratefully acknowledges the award of a grant from the Australian Research Grants Committee which enabled her to visit the site, together with the invaluable assistance of Mr. C. E. Dortch and Dr. D. Merrilees. Help and criticism from Mr. A. Baynes, Dr. R. Frank and Dr. J. Jennings have also been beneficial. Laboratory and computing facilities were kindly provided by the Department of Archaeology, University of Southampton, and the Institute of Archaeology, University of Oxford.

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The Dunsborough implement: an Aboriginal biface from southwestern Australia

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Manuscript received 21 June, 1977; accepted 21 June, 1977

Abstract

A chert artifact superficially resembling a Palaeolithic biface has been found at Dunsborough, Western Australia. It is distinctively coloured, but otherwise resembles petrographically the Aboriginal artifacts of Eocene bryozoan chert previously described from southwestern Australia. The presence of *Nothofagidites* sp. and *Haloragacidites harrisii* (Couper) Harris, rules out European origin. Other microfossils indicate Early or Middle Eocene age for the chert. The Dunsborough implement, and another biface from a nearby site, are made of rock probably quarried west of the present Western Australian coast in the late Pleistocene or early Holocene, when sea level was lower. The investigation emphasizes the potential value of palynological examination of chert implements particularly when exotic origin is suspected.

Introduction

Over the past half century, numerous large bifacially flaked stone implements have been found in Australia, particularly at sites in the coastal districts of southeastern South Australia and western Victoria (Fig. 1). Most are of Aboriginal origin, but several are European, the best known being Palaeolithic implements picked out of English flint ballast dumped by sailing ships at Port Lincoln, South Australia (Fig. 1). The latter implements are displayed at the South Australian Museum.

The most controversial of these bifacially flaked pieces is the Scaddan implement (Fig. 2), a flint biface closely resembling an Acheulian hand axe, which was collected at Scaddan near the south coast of Western Australia (Fig. 1). The specimen was early recognised as problematical (Noone 1943), though Tindale regarded it as an Aboriginal artifact (Tindale 1941, p. 145; 1949, p. 165). A decade later McCarthy stated that the Scaddan implement resembled "more closely the flint *coup-de-poing* from Europe, examples of which, brought here by various people or in ships' ballast, have found their way into strange places in Australia." (McCarthy 1958, p. 178).

In 1976 two of us (CED, JEG) carried out an archaeological and petrological study of the Scaddan implement (Dortch & Glover in press) and concluded from its technology and style, its stone texture, surface patination and colour, and its rolled condition, that it is much more likely to be of English than Australian origin. Unfortunately the contained microfossils were poorly preserved, and gave no conclusive information about the origin and age of the stone.

Soon after the analysis of the Scaddan implement, another large flint or chert biface somewhat resembling a Palaeolithic hand axe was found by a schoolboy, Clayton Wholley, at the small coastal resort of Dunsborough some 200 km south of Perth (Fig. 1). The implement was in a vacant block of land from which the vegetation had been partly cleared in preparation for building. When first seen it was partly exposed in the surface of a sandy deposit which has been extensively disturbed during the European era.

Now, artifacts of Middle or Late Eocene chert are of particular interest in the pre-history of the Perth Basin and adjacent areas. They characterize late Pleistocene and early Holocene assemblages, but their source has never been found because it was probably submerged about 6000 BP (Glover 1975). Consequently the presence or absence of these artifacts in an assemblage provides archaeologists with a pointer to its age.

There are therefore several reasons for reporting on the Dunsborough implement in detail, and establishing the age of the chert. This paper gives an archaeological description of the Dunsborough implement, describes its petrology and palynology, and discusses its history and its relationship to other Western Australian chert artifacts. In particular, the investigation shows how palynological techniques may illuminate the origin of chert implements, and how they can distinguish transported Acheulian hand axes from Australian implements of similar appearance. The responsibilities of the authors are as follows: archaeology, CED; petrology, JEG; palynology, BEB.

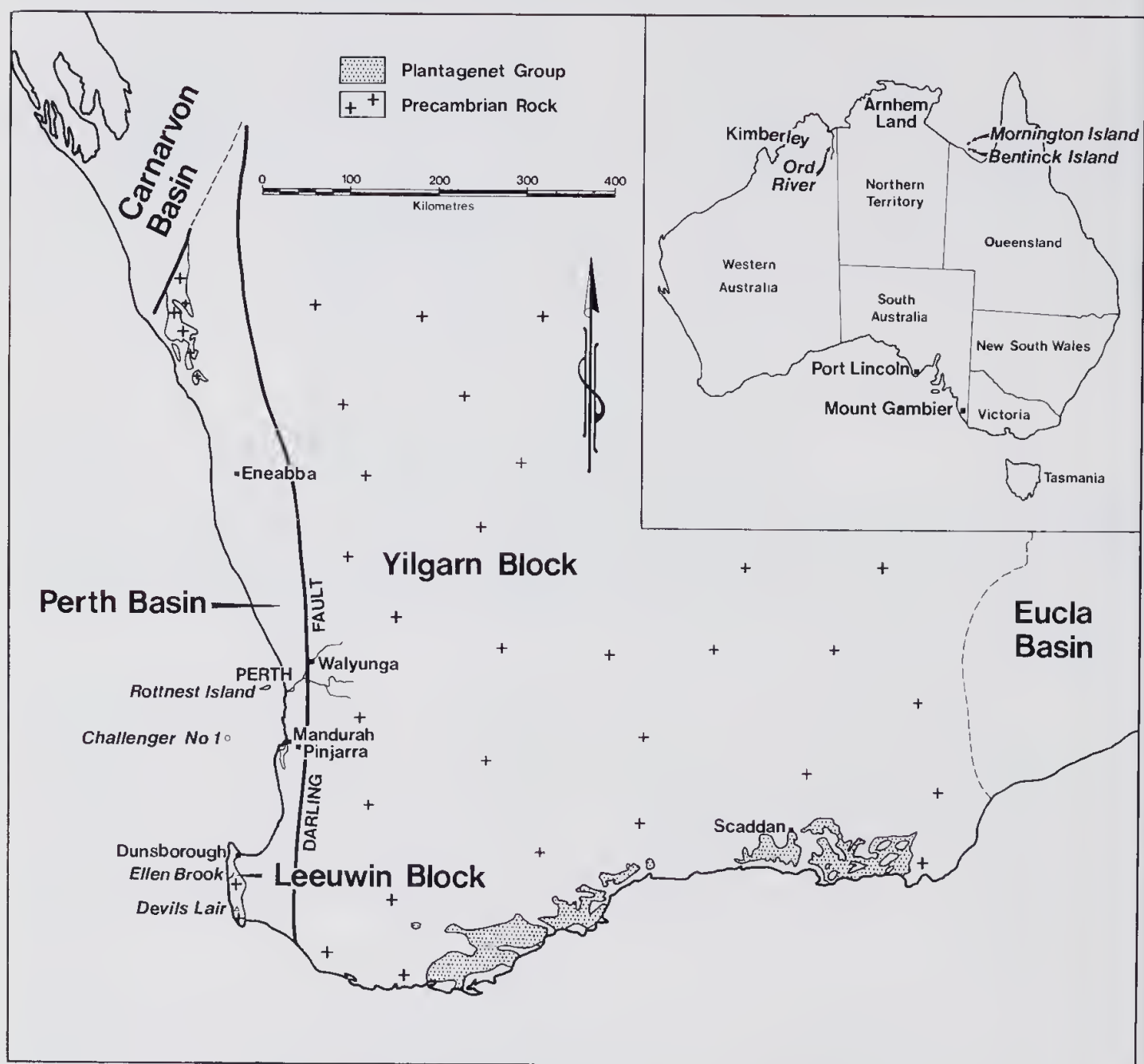


Figure 1.—Map showing localities mentioned in the text.

Archaeological description

The Dunsborough implement (Fig. 3) is a complete, invasively flaked chert biface. It weighs approximately 300 g and has the following dimensions; length 106 mm; width 83 mm; and thickness 46 mm. In plan view or outline the piece is sub-oval, and it is roughly elliptical in section. About one third of one face (Fig. 3, right) retains a cortex surface. A single positive conchoidal fracture extends over much of the opposing face (Fig. 3, left) and so the implement is probably made on a single large flake. The right-hand and lower edges of the piece (Fig. 3, right) are broad and thick with deeply biting, bold flake scars, whereas the left-hand and upper left edges shown in the same figure have much more

acutely angled edges produced by shallower and more invasive bifacial flaking. (The latter angles are not apparent in the side view shown in Fig. 3, centre.)

The piece shows very clear abrading and crushing, i.e. multiple, overlapping and very small (0.5-5 mm) conchoidal fractures, on parts of its lateral edges and particularly on the low ridge running down the lower centre of the face shown in Figure 3, right. The crushing on this ridge encroaches over the adjacent flake scar ridges and facets, clearly post-dating them. Most of the other flake scar ridges on both faces are undamaged or only very slightly so. The two fan-shaped scars extending left of the abraded ridge in Figure 3 right, and also several much smaller scars immediately

to the right of the ridge, seem to originate from a single source of percussion. Possibly then this face was used as an anvil or hammer surface; on the other hand these scars could be the result of glancing percussion occurring when the piece lay with its face exposed to stones carried in high-velocity water flow. The proximity of these flake scars to the abraded central ridge, the virtual absence of abrading or battering on the opposite face of the piece (Fig. 3, left), and its differentially abraded lateral edges, all suggest that they are the result of use, or perhaps a combination of use and some natural abrasion.

The fragmentary remains of the calcareous shell of a marine invertebrate adhere to one face (Fig. 3, right, lower right corner). As the shell is of recent origin the implement must have been submerged only a short time before being found and so the piece was not in primary position when collected.

Stylistically the Dunsborough implement does not closely resemble any of the classic forms of Acheulian or Mousterian hand axes from north-western Europe (cf. Bordes 1961; Roe 1968; Wymer 1968). However its surface colouration and texture, size, and general morphology place it within the range of biface variation known from European Palaeolithic assemblages.

Petrology

The surface colour of the implement ranges from medium bluish grey (5B5/1) to greenish grey (5GY6/1) and yellowish grey (5Y7/2) (See Rock-color Chart Committee 1963 for comparative colours, and explanation of the symbols). A section through the implement shows that it is rimmed locally by a bluish white (5B9/1) patina up to 2 mm thick. Inward from the patina, the core ranges from medium grey (N5) to very light grey (N8), and there is a small, light brown (5YR6/4) area about 1 cm long stained by iron oxide.

The rock is a fossiliferous chert with abundant silicified Bryozoa and Foraminifera, in a matrix of cryptocrystalline silica (average grain size <0.01 mm in diameter). There are numerous patches of coarser chalcedonic quartz (average grain diameter 0.03 mm), and some tests have an infilling of coarse, drusy chalcedony with a core of granular quartz. Siliceous spicules are also present, but their original composition is uncertain.

A feature of many of the silicified tests is a very fine fringe, generally directed inward from the test wall. The fringe is formed of colourless, roughly wedge-shaped bodies, commonly about 0.01 mm long, with a pronounced nega-

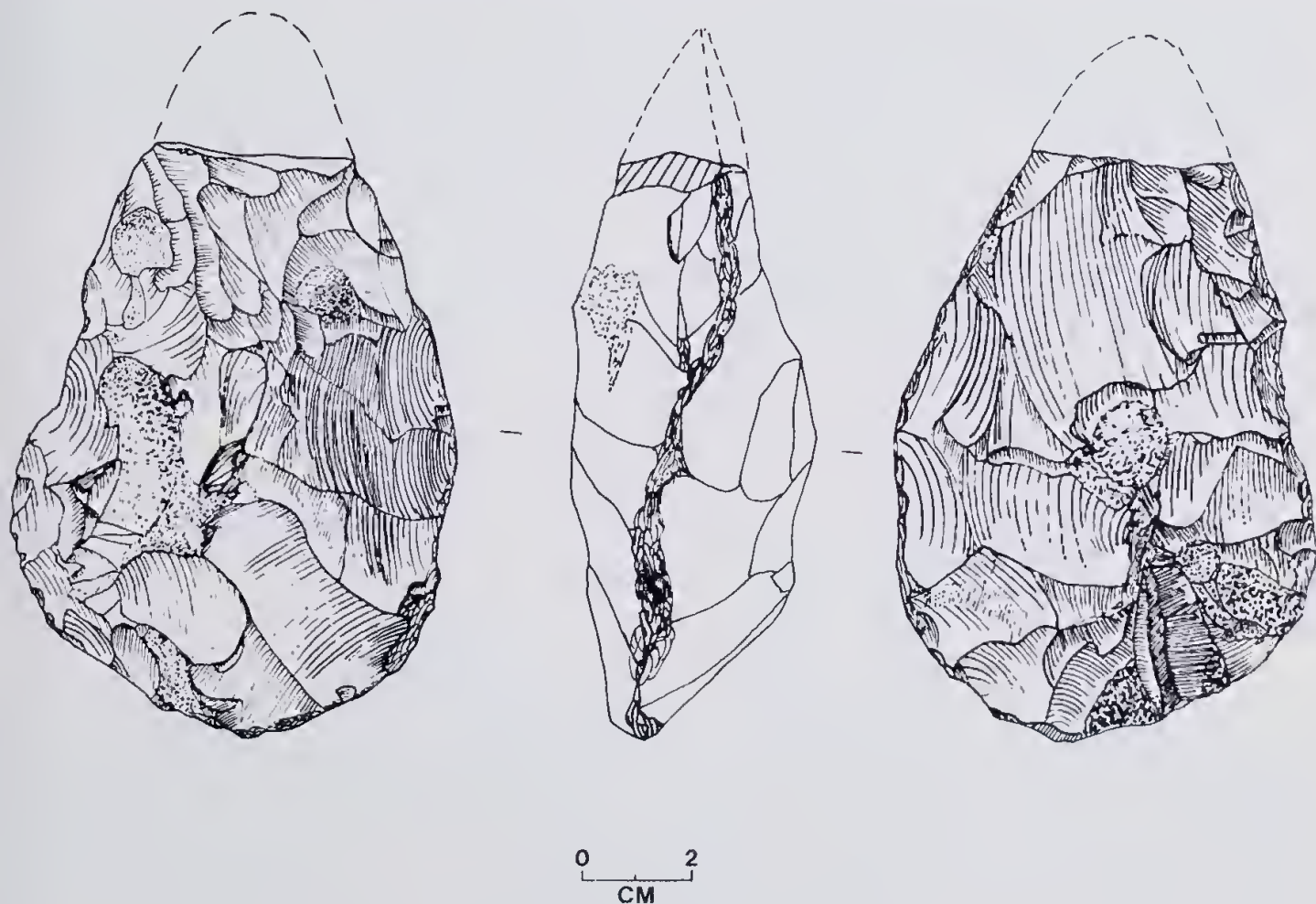


Figure 2.—The Scaddan implement.

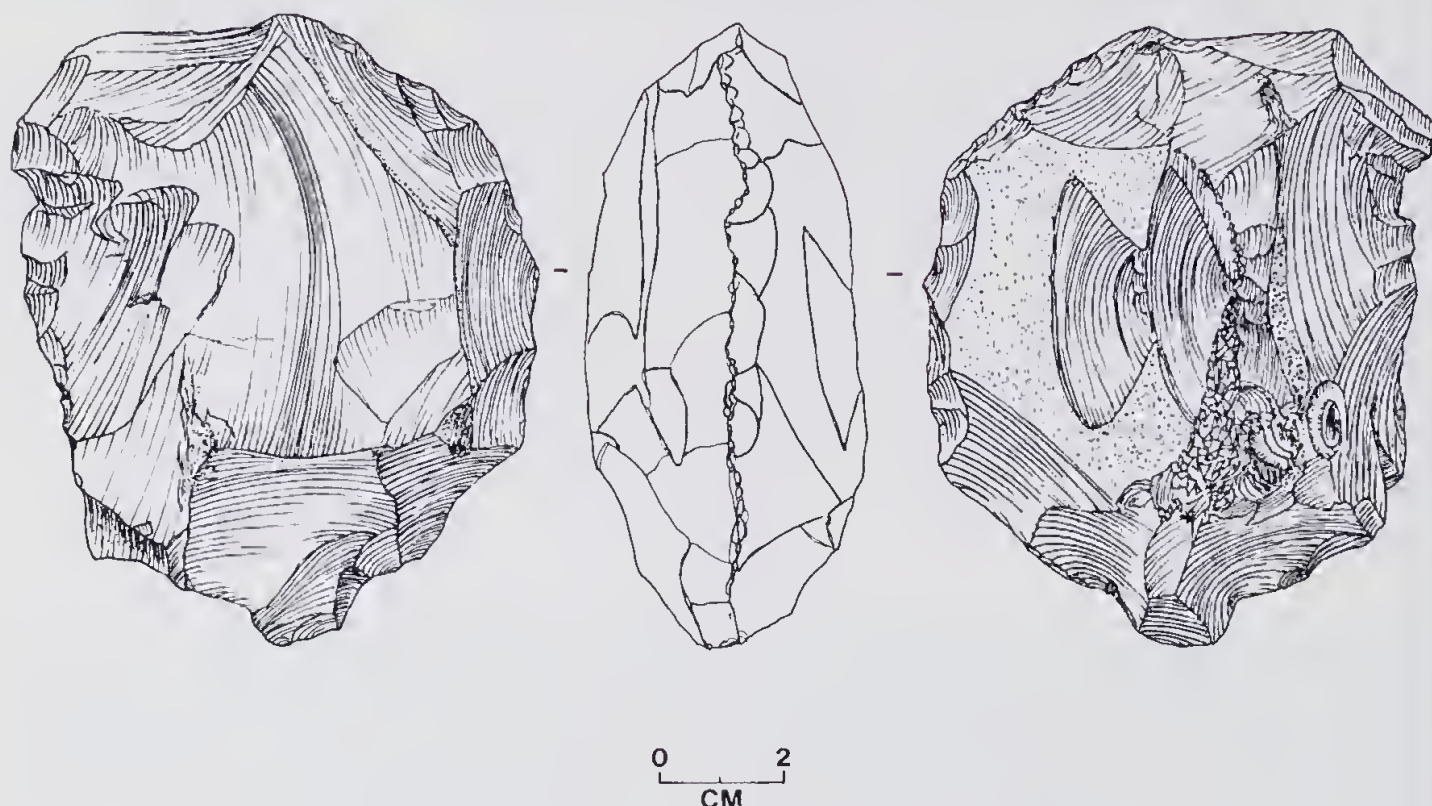


Figure 3.—The Dunsborough implement.

tive relief that causes them to appear dark under low magnification. The bodies were first thought to be opal, but their negative relief is too strong. Their drusy habit suggests that they are cavities left after solution of drusy calcite that was not replaced by silica. Whatever their origin, these features are common in Western Australian Eocene chert.

Other material in the chert includes rare glauconite pellets, silt-sized clastic quartz, grey, finely disseminated clay, and fragments of plant microfossils.

Comparison with chert flakes

The Dunsborough implement was found in an area from which flakes of chert, quartzite, mylonitic rock and silcrete were recovered. Quartzite is quite abundant. A broken pebble of granitic rock was also collected.

Chert flakes are common in the Perth Basin, particularly in the western part of a belt extending between Eneabba and Mandurah (Glover 1975). Many of these flakes contain Eocene Bryozoa, and the Middle and Late Eocene foraminifer *Mastinella chapmani* Glaessner and Wade has been identified in two of them (Glover & Cockbain 1971). More recently, concentrations of similar flakes have been found in blow-outs in sand on the western part of the Leeuwin Block. Petrologically, there is nothing to distinguish the chert flakes found at Dunsborough, or elsewhere in the Perth Basin or Leeuwin Block, from the chert of the implement. There is, however, a difference in surface colour. Most of the flakes in the Perth

Basin range from white, through shades of grey, brown and orange, whereas the implement has blue and green tints noted elsewhere only in two of the Dunsborough flakes. The significance of these colours is uncertain, because the colour of many flakes seems to be at least partly influenced by the colouration of the sand in which they are found.

Palynology

Treatment

Inorganic and oxidisable organic materials were removed by boiling about 2 g of the crushed chert in HF, followed by warming the residue in 10% HCl and oxidising the acid-insoluble fraction with concentrated HNO₃. A small quantity of microscopic plant fragments remained. Because the number of identifiable plant microfossils in the final residue was small, three separate preparations were carried out to guard against misinterpretations resulting from laboratory contamination.

Plant microfossils

Plant microfossils were recovered from each of the three preparations. Small cuticular pieces and woody tissues predominated, but fragmental dinoflagellates of the *Spiniferites*-type were fairly common. No more than about 10 identifiable microfossils were found in each of the residues. However, the assemblages were consistent and the same forms were recognised in all three. It was therefore concluded that the plant microfossils were derived entirely from the material of the biface. All the species identified are listed below:

Spores and pollen:

Cyathidites sp.
Haloragacidites harrisii (Couper) Harris
Nothofagidites sp. (*Nothofagus brassii*-Group)

Microplankton:

Leiosphaeridia sp.
Veryhachium sp.
Homotryblium floripes (Deflandre & Cookson)
Stover
Spiniferites sp.
Deflandrea sp. (hypotract only)
Rottnestia borussica (Eisenack) Cookson & Eisenack
Wetzeliella sp. cf. *W. lineidentata* Cookson & Eisenack
Leptodinium maculatum Cookson & Eisenack.
? *Schematophora* sp.
Baltisphaeridium paucifurcatum (Cookson & Eisenack) Downie & Sarjeant

Reworked microfossils:

Microbaculispora tentula Tiwari (Permian)
Plicatipollenites sp. (Lower Permian)
Cycadopites cymbatus (Balme & Hennelly)
Segroves (Lower Permian)

The presence of *Nothofagidites* sp. and *Haloragacidites harrisii* rule out any possibility that the chert is European. Both these species are typically southern hemisphere forms that range from the Late Cretaceous to the present. In Western Australia they are frequently associated in Eocene assemblages and in this State *Nothofagidites* has not yet been recorded from sediments older than Eocene.

Wetzeliella is unknown from pre-Tertiary strata. Its first appearance is in the Early Palaeocene of North America and its latest occurrence in the Middle Miocene of Europe (Harker & Sarjeant 1975). In Australia it particularly characterises Eocene sediments. Stover (1975) discussed the stratigraphic distribution of *Homotryblium floripes* which was recorded by Cookson and Eisenack (1961) from the Kings Park Formation, between 451 and 486 m in the Rottnest Island bore. Current opinion regards this section of the Kings Park Formation as Early Eocene (Cockbain & Ingram quoted by Quilty 1974). According to Stover, the species ranges into the Early Miocene. The type material of *Leptodinium maculatum* Cookson & Eisenack also came from the interval 453-486 m in the Rottnest Island bore. This is the only published record from Australia, although a similar form occurs in the Lower and Middle Eocene of Europe.

The other dinoflagellates present are all consistent with an Early Tertiary age, although they are less important, either because they are long-ranging forms, or because the identifications are uncertain.

Considering the sum of evidence, the most likely age of the assemblage is Early or Middle Eocene. Comparisons with published data from Australia further strengthen this conclusion. In particular, there are striking similarities between the microfossil assemblage from the biface and those recovered from sediments in the interval 453-485 m in the Rottnest Island bore (Cookson & Eisenack 1961; Hassell & Kneebone 1960). All the plant microfossils listed, or closely similar forms, have been previously recorded from samples in this interval,

with the exception of reworked Permian microfossils. As an additional check, material from the Rottnest Island bore, prepared by Dr C. W. Hassell and retained in the collections of the Department of Geology, University of Western Australia, was re-examined. Rare Permian saccate pollen grains and a specimen of *Microbaculispora tentula* Tiwari were found in a smear mount prepared from a core cut in the interval 451-470 m. The source of these reworked Permian pollen grains is obscure. No exposures or shallow subsurface occurrence of Permian strata are known in the vicinity of Rottnest Island. As reworked Cretaceous pollen are also present in the Tertiary assemblages, it is possible that the Permian forms represent second-cycle reworking, from Mesozoic sediments.

In summary, the palynological evidence points irresistibly to the conclusion that the biface is made of Early or Middle Eocene chert, obtained either from the Kings Park Formation or a unit correlating with it.

Stratigraphic source of the chert

The source of the Dunsborough implement, and of petrographically similar chert pieces, is bound up with the distribution of Eocene rocks in the southwest of Western Australia. There is only one sequence of Eocene rocks cropping out in the region, namely the Late Eocene Plantagenet Group, which is distributed within an irregular belt along the south coast, and is a local source of chert for artifacts. Colloform opal is common in chert flakes from the Plantagenet Group, but is absent from flakes on the Leeuwin Block, and in the central and northern Perth Basin.

The only unit described from the Perth Basin that contains Eocene rocks is the sub-surface, Palaeocene—Early Eocene Kings Park Formation (Quilty 1974). However, palynological evidence suggests that the interval from this formation intersected between 451 and 486 m in the Rottnest Island bore extends to the Middle Eocene. In addition, Quilty (pers. comm. 1975) has recognized unnamed Late Eocene strata, including chert, from the interval between 510 and 590 m in WAPET's Challenger No. 1 well, about 60 km west of Mandurah. There are clearly gaps in our understanding of the Eocene stratigraphy of the Perth Basin, and published information is far from comprehensive.

The chert of flakes from the Perth Basin has been dated as Middle or Late Eocene from Bryozoa and Foraminifera. It has been argued that the concentrations of Perth Basin chert flakes in the Eneabba-Mandurah belt, and their increase in frequency westward, point to derivation from westward sources that were submerged as the sea rose to its present level (Glover 1975). More recently, independent radiocarbon evidence from excavations at Wal-yunga shows that the source of chert for artifacts was eliminated between 6135 ± 160 and 3220 ± 100 years ago (Pearce, pers. comm. 1976). Recent work has also revealed additional con-

centrations of chert flakes near the western margin of the Leeuwin Block, and it can be argued that those also come from the west.

The flora of the Dunsborough implement correlates well with that of the Early or Middle Eocene rocks in the interval of Kings Park Formation between 451 and 486 m in the Rott-nest Island bore. As these rocks do not crop out, the source of the implement is best sought seaward. Rocks of the Kings Park Formation would have been exposed in the valley of the ancestral Swan, and probably elsewhere in windows through the veneer of later rocks. The Kings Park Formation lenses out around the latitude of Pinjarra, and off-shore rocks of equivalent age in the Dunsborough region may have yielded the implement.

Unfortunately, the chert flakes assumed from the Bryozoa and Foraminifera to be Middle or Late Eocene, have not yielded palynological residues sufficiently well preserved to compare with the residues from the Dunsborough implement. The various flakes and the Dunsborough implement may therefore have come from rocks of the same age, or of somewhat different age and stratigraphic position within the Eocene Series.

Discussion

The best documented concentration of large, invasively flaked flint bifaces on the Australian continent is in the assemblages noted earlier from sites in southeastern South Australia and western Victoria. Tindale (1941) designated these assemblages as the "Gambierian" industry, because there is a concentration of them near Mt Gambier, South Australia. Illustrations of selected specimens of flint bifaces from this district (Mitchell 1949, Figs. 32, 33; Stapleton 1945, Figs. 1, 10, 11) clearly show them to be remarkably similar to Old World Palaeolithic hand axes, a fact noted by the two foregoing and other authors (McCarthy 1940, p. 30-33; Mulvaney 1961, p. 71-72; Tindale 1941, p. 145, 165.).

The regional stone industries of Kimberley and Arnhem Land also contain a series of bifacially flaked points and axes in which there are a few pieces resembling Lower or Middle Palaeolithic bifaces. Dortch & Glover (in press) illustrate an ethnographic example of one of these from the Ord valley in east Kimberley. Other large bifaces were collected by the late E. J. Brandl in Arnhem land.

The large picks or "oyster stones" from Bentinck and Mornington Islands, Queensland (Fig. 1), which Tindale (1949, p. 161) describes as being "of crude biface form", in some cases at least are square or rounded in section (Tindale 1949, Figs 6, 11) and so are not truly bifacial. We agree with McCarthy (1958, p. 178-9) that these pieces do not resemble the developed "hand axe" or *coup-de-poing* of the Old World Palaeolithic. Instead they seem to be similar to the more crudely flaked specimens of the *biface abbevillien* and the *pic* of the Lower Palaeolithic of France (cf. Bordes 1961, Plates 88, 90, 91).

Large bifaces, generally of edge-ground form, are known from sites in many parts of Australia (McCarthy, Bramell & Noone 1946, p. 15, 49), including the southwest (Akerman 1973; Ride 1958). However, apart from the "Gambierian" concentration and the few specimens from Kimberley and Arnhem Land, there do not seem to be any other clear regional series of large bifaces resembling those of the Old World Palaeolithic.

Nevertheless the Dunsborough implement is not the only unequivocally indigenous, large biface from the southwest. In October 1976 one of us (CED) recovered a broken chert biface from a coastal blow-out at Ellen Brook 34 km south of Dunsborough (Fig. 1). Numerous chert and quartz artifacts were exposed in the blow-out, and typological and petrological aspects of the assemblage suggest that it is attributable to the early phase of industries identified in the southwest (Dortch 1977; Glover 1975; Hallam 1972).

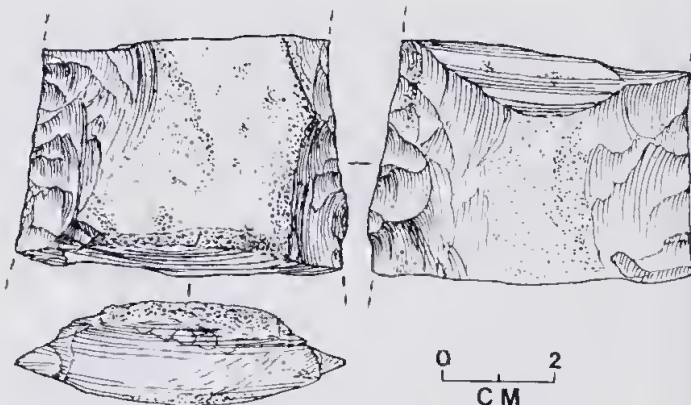


Figure 4.—The Ellen Brook biface.

The Ellen Brook biface (Fig. 4) is an invasively flaked fragment of tabular chert in which both extremities are broken off, perhaps deliberately. The piece is neatly elliptical in section, and both lateral edges are delicately flaked. The specimen is made of the distinctive Eocene bryozoan chert which as noted earlier, characterized southwestern late Pleistocene and early Holocene assemblages.

Part of the significance of the Ellen Brook biface is that, unlike the Dunsborough implement, it clearly shows that southwestern Aborigines were capable of careful, controlled invasive flaking resembling that produced by the "soft-hammer" technique (Bordes 1961, p. 8). Together the Ellen Brook and Dunsborough bifaces confirm Tindale's view that large bifaces are indigenous to the southwest (Tindale 1949, p. 165). However, Tindale based his opinion on the single find of the Scaddan implement (Fig. 2), a specimen which we believe to be probably English in origin. At the same time the view that the Scaddan implement is a "typological and technological anomaly" in southwestern Australia (Dortch and Glover in press) must be amended. Thus, pieces similar to the Scaddan implement were made by

southwestern Aborigines, if only rarely. The probable early Holocene or late Pleistocene ages and early-phase associations of both the Dunsborough and Ellen Brook implements suggest that other specimens resembling Old World Palaeolithic bifaces are likely to be identified in early-phase assemblages in the southwest.

This discussion should end with a note on techniques. Petrology has long been used with some success to trace the history of European and Australian artifacts, but it is not always easy to distinguish between cherts by petrology. Invertebrate fossils can be useful. Floral remains, despite their toughness, do not always survive silicification, as in the Scaddan implement. On the other hand, floral residues from the Dunsborough implement have unequivocally shown its Australian origin. Palynological examination should therefore be attempted whenever an exotic origin is suspected.

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New species of fossil nonmarine molluscs from Western Australia and evidence of late Quaternary climatic change in the Shark Bay district

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Manuscript received 21 June, 1977; accepted 21 June, 1977.

Abstract

The new species *Coziella roeae* sp. nov. (Prosobranchia: Hydrobiidae), *Bothriembryon gardneri* sp. nov., *B. consors* sp. nov., *B. douglasi* sp. nov. and *B. ridei* sp. nov. (Stylommatophora: Bulimulidae) are described and figured. All occurrences are believed to be of Pleistocene age.

Coziella roeae sp. nov. was obtained from lacustrine deposits in the Beermullah district and represents the first fossil species to be recorded for the genus.

The four new species of *Bothriembryon* snails come from fossil soils in the Point d'Entrecasteaux and Shark Bay districts. Those from the former locality, *B. gardneri* sp. nov. and *B. consors* sp. nov., are related ancestrally to living species. The two Shark Bay species, *B. douglasi* sp. nov. and *B. ridei* sp. nov., have no known living descendants. Their extinction, and the apparent subsequent appearance of camaenid snails in the district, are interpreted as evidence of a period of severe regional aridity during the late Pleistocene.

Introduction

This paper describes five new species of molluscs, one freshwater and four terrestrial, from the fossil collections of the Western Australian Museum (WAM) and the Field Museum of Natural History, Chicago (FMNH). The material studied came from three widely separated areas in southwestern Australia (Fig. 1).

Coziella roeae sp. nov. was obtained in sediments collected from wells, seismic boreholes and other shallow excavations in the Beermullah district, 80 km north of Perth, by Mrs. R. Roe, of "Benalong", Beermullah.

From 1941 to 1976, fossil snail shells have been obtained by a number of collectors from exposures, both natural and man-made, of lithified fossil soils associated with aeolian calcarenite at Point d'Entrecasteaux on the coast of Western Australia south-southeast of the town of Northcliffe. The deposit contains at least eight different species of land snails, of which two, *Bothriembryon gardneri* sp. nov. and *B. consors* sp. nov., are described below.

Collections of land snails from widely dispersed fossil soils in the Shark Bay district, resembling the Depuch Formation, have been found to contain two species of *Bothriembryon* distinct from any now living. These species, which appear to be allopatric, are described as *B. douglasi* sp. nov. and *B. ridei* sp. nov.

A comparison of what is known of modern and fossil land snail distributions in the Shark Bay district suggests that a period of glacioeustatic low sea levels during the late Pleistocene was marked by the extinction of two *Bothriem-*

bryon species and the subsequent local establishment of up to four species of arid-adapted camaenid snails. These apparent faunal changes are considered to reflect a regional climatic shift towards increased aridity. A relative climatic amelioration appears to have eventuated in the wake of the Flandrian (Holocene) transgression, possibly reflecting the strengthening of maritime influences in the area.

Systematic descriptions

Class Gastropoda
Subclass Prosobranchia
Order Mesogastropoda
Superfamily Rissoacea
Family Hydrobiidae

Genus *Coziella* E. A. Smith, 1894.

Coziella Smith, 1894. *Proc. malac. Soc. Lond.* 1: 98.
Coziella Smith; Ludbrook, 1956. *Trans. roy. Soc. S. Aust.* 7: 41 (with synonymy).

Type species (by original designation): *Truncatella striatula* Menke.

From consideration of the shell characters, *Coziella* has been referred to a diversity of families, e.g., Hydrobiidae subfamily Truncatellinae (Thiele 1931; Macpherson 1957), Coxiellidae (Iredale 1943), Truncatellidae (Cotton 1959; McMichael 1967) and Assinincidae (Ludbrook 1956). Living animals of *C. striatula* have been examined by Dr. G. M. Davis of Philadelphia who states (pers. comm., May 1972) that, in characters of the head-foot morphology, mode of progression, form of the eyes and tentacles and the radula, they show affinity with the Hydrobiidae and not the Truncatellidae; clarification of the subfamily position requires further study.

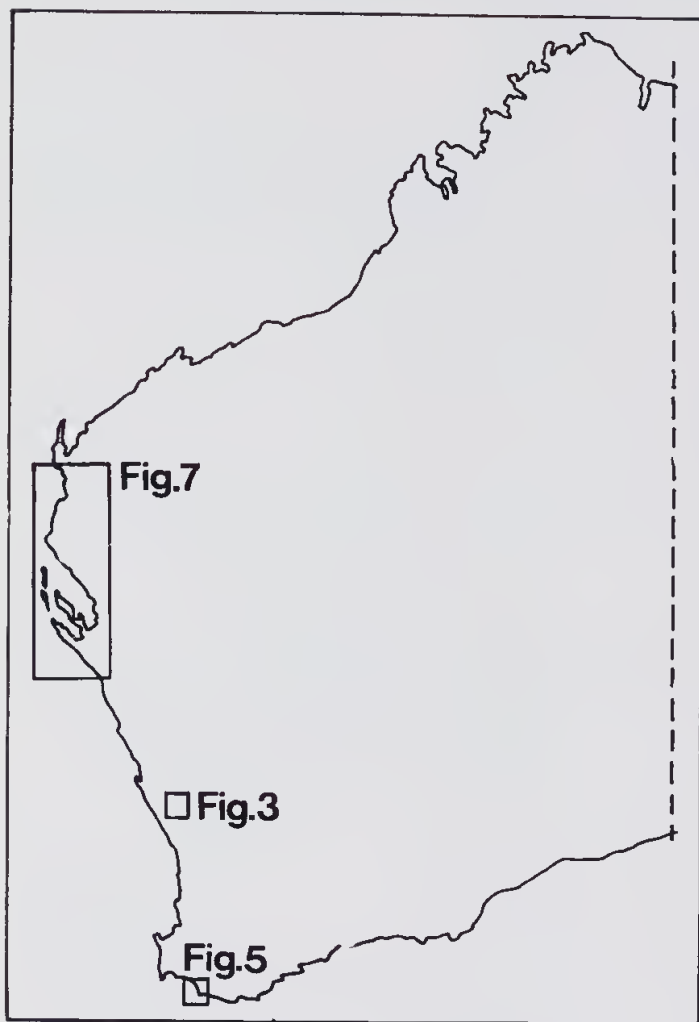


Figure 1.—Western Australia, areas studied.

***Coxiella roeae* sp. nov.**
(Fig. 3)

Material. Holotype WAM 73.4. Paratypes WAM 73.5 (40 shells). Other topotypic reference material WAM 73.6, 73.7, 73.8, 73.9 (5 560 shells). All of this material was collected originally as a single sample.

Type locality. Beermullah, Western Australia. Lat. $31^{\circ} 11' S$, long. $115^{\circ} 42' E$. "Benalong" bore at northern part of Swan Location 5261, about 0.5 km east of Location 2680, ("Pin Pin"); 4.6–4.9 m below ground surface (Fig. 2).

Diagnosis. A medium-sized *Coxiella* up to 17 mm high, of somewhat variable form, elongate-conical or turriculate, with height about twice the maximum diameter. Protoconch smooth, paucispiral, either present or absent through decollation, in which case a septum is formed. Whorls convexly rounded, flattened, shouldered or carinate; sometimes cingulate above the periphery, with sutures impressed or incised. Sculpture of irregular, colabral growth rugae and very fine, close, spiral striae, becoming obsolete on the base and occasionally entirely absent. Umbilicus present, small in juveniles, becoming wide (for the genus) in mature shells. Aperture ovate to quadrate, according to the degree of carination; often with persistent yellow-brown pigmentation within. Shells white externally.

Description of holotype. Shell of medium size, elongate-conical, of 7.8 whorls in a height of 9.6 mm, maximum diameter 5.5 mm. Apex intact, protoconch smooth, paucispiral; spire whorls convexly rounded, the last whorl slightly flattened, sutures impressed. Sculpture of irregular, colabral growth rugae and very fine, close, spiral striae, becoming obsolete on the base. Umbilicus open, small. Aperture ovate, oblique and continuous, the columellar lip everted; faintly yellow-brown within. Shell white externally.

Observations. Of the described species of *Coxiella*, (Macpherson 1957), the fossil species is closest in general shell proportions to *C. pyrrhostoma* (Cox), though not attaining the height of that species (17 against 20 mm). Other similarities are the presence of contrasting pigmentation within the aperture and the spiral striation. Some rugose, shouldered or cingulate shells of *roeae* recall specimens of *C. glauerti* Macpherson from the Esperance-Israelite Bay district. Examination of a range of specimens from that area collected since Macpherson's revision of the genus suggests to the writer that *glauerti* may be no more than a localised gerontic form of *pyrrhostoma*.

C. roeae differs markedly from *pyrrhostoma* and most other species of *Coxiella* in the relatively late onset of decollation and also in the limited extent to which this is usually manifest. This is shown among the fossils by the presence of a substantial proportion of mature shells having either intact or very slightly decollate apices. In *pyrrhostoma* by contrast, decollation appears to occur early in growth when the shell is 4–5 mm high and recurs subsequently a number of times. Juvenile, non-decollate shells of *pyrrhostoma* have a subcylindrical form in contrast to the ovate-conical form of young *roeae*. Occasional shells of *roeae* exhibit a more extensive decollation, comparable to that of extant species. Carination of the whorls in a proportion of shells distinguishes *roeae* from all other congeners. The new species is considerably more variable in shell characters than any other *Coxiella*; however the extreme forms are connected by intermediates and all are considered to represent a single species. The paratype series, a selection of which is illustrated (Fig. 2C–N), demonstrates this variation.

The carinate forms of *C. roeae* bear a remarkable resemblance to shells of *Pyrgula barroisi* Dautzenberg (Truncatellidae) from the Sea of Galilee, figured by Tchernov (1975, p. 156, Figs. 5, 6, 9).

The species is named after Mrs. R. Roe, who presented to the Western Australian Museum all of the material and collecting data utilised in this study.

Geographic range. The present species has been collected by Mrs. Roe from spoil from a series of bores, wells, seismic shotholes and other shallow excavations within 12 km to the south and east of the type locality and from a surface outcrop on the eastern side of Beermullah Lake some 8.5 km to the east. The positions

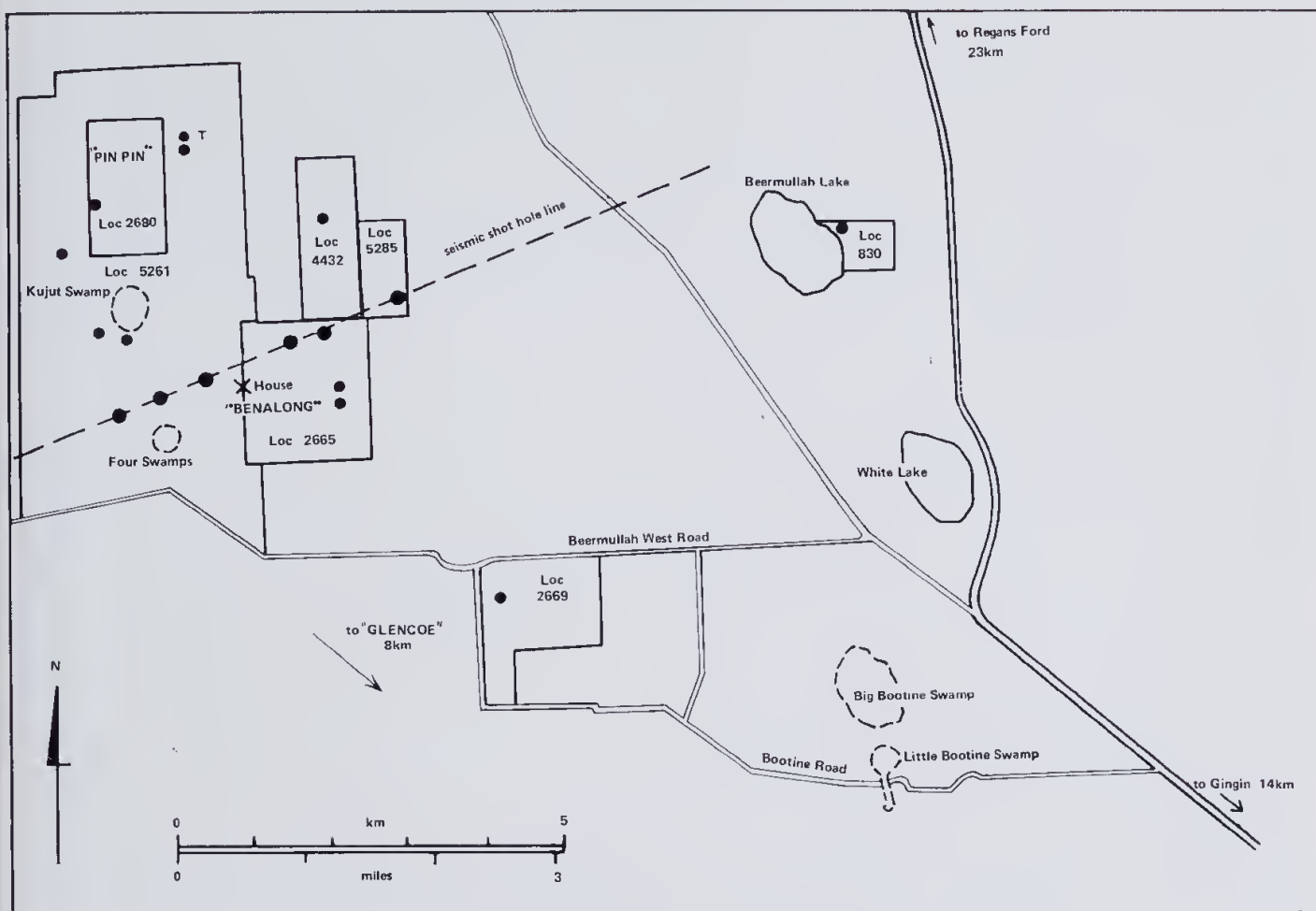


Figure 2.—Beermullah district. *Coxiella roae* localities. Type locality T.

of these localities are shown in Fig. 2; the greatest depth sampled was 13.7 m below the ground surface. Hosking and Greave (1936, p. 106) report "hard compact limestone containing small mollusc shells of presumably Tertiary age" from near "Glencoe" homestead, Beermullah. This property, now known as "Mirilla", lies about 8 km southeast of known occurrences of *C. roae* and may contain an extension of the same *Coxiella* beds. The data suggest that one or more extensive lakes may have occupied the area at the time of deposition. The presence of occasional associated fossil shells of the pond snail genera *Physastra* and *Gyraulus* (e.g. WAM 73.10, 71.984) with *C. roae* indicates that these water bodies were more likely to have been fresh rather than saline at the time of deposition.

Stratigraphic range. The precise age of the present material cannot as yet be determined but marine mollusc shells (WAM 73.98-104, 73.106-7) from a bore on Swan Location 2680 ("Pin Pin", Fig. 2), close to the type locality of *C. roae* but from between 27.4-36.6 m below the ground surface are, in the writer's view, of probable Pliocene age. If so, then the overlying lacustrine beds containing *C. roae* were probably laid down during the Pleistocene. Apart from late Quaternary deposits around Lake Eyre, South Australia, containing fossils of the

extant *C. gilesi* (Angas) (Ludbrook 1956; King 1956), little has been established of the geologic history of the genus.

Subclass Euthyneura
Order Stylommatophora
Superfamily Bulimulacea
Family Bulimulidae

Genus *Bothriembryon* Pilsbry, 1894.

Bothriembryon Pilsbry, 1894, *Nautilus* 8:35-36.
Bothriembryon Pilsbry; Kendrick and Wilson, 1975.
Rec. West. Aust. Mus. 3:312 (with synonymy and redescription).

Type species (by original designation): *Bulimus melo* (Quoy and Gaimard) = *Helix melo* Quoy and Gaimard.

***Bothriembryon gardneri* sp. nov.**
(Fig. 4, A-E)

Material. Holotype WAM 70.1603a. Paratypes WAM 70.1603b and c, 2 shells; 66.794a and b, 2 shells embedded in a laminar piece of brown calcarenite; 66.798a, h and w, 3 shells; FMNH 194694/3, 3 shells. Other reference material WAM 70.1603d to p, 13 topotypes; 66.795, 1 shell in hard, brown calcarenite; 66.796, 2 shells in hard, brown calcarenite; 66.797, 2 shells in a large, laminar piece of brown calcarenite; 66.798, 18 complete and 31 fragmentary shells; 62.196, 1 shell in brown calcarenite; 62.197, 1

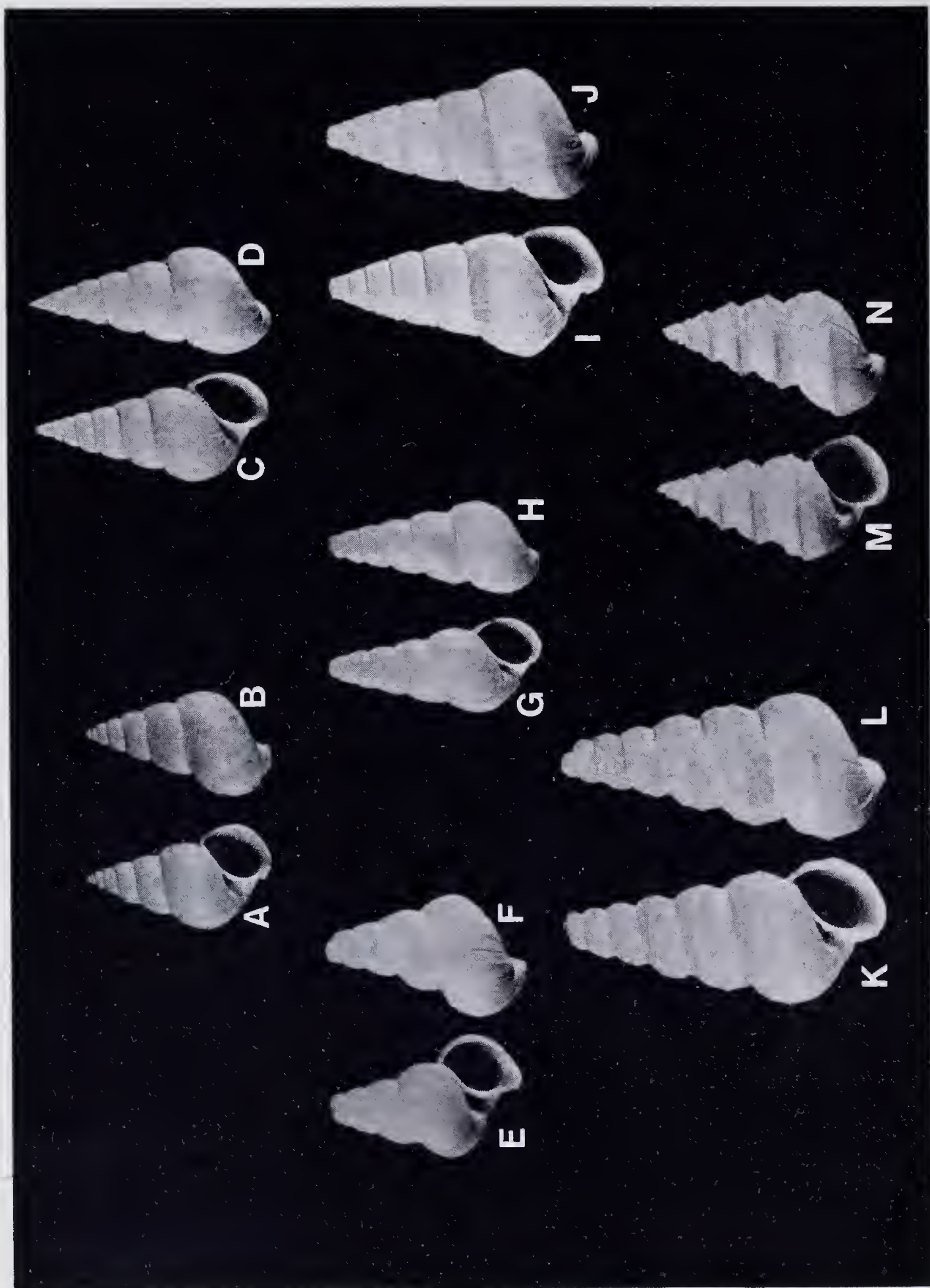


Figure 3.—*Coxiella rocae* sp. nov. A, B.—Holotype, WAM 73.4. C-N.—Paratypes, 73.5 a-f. All x 3.

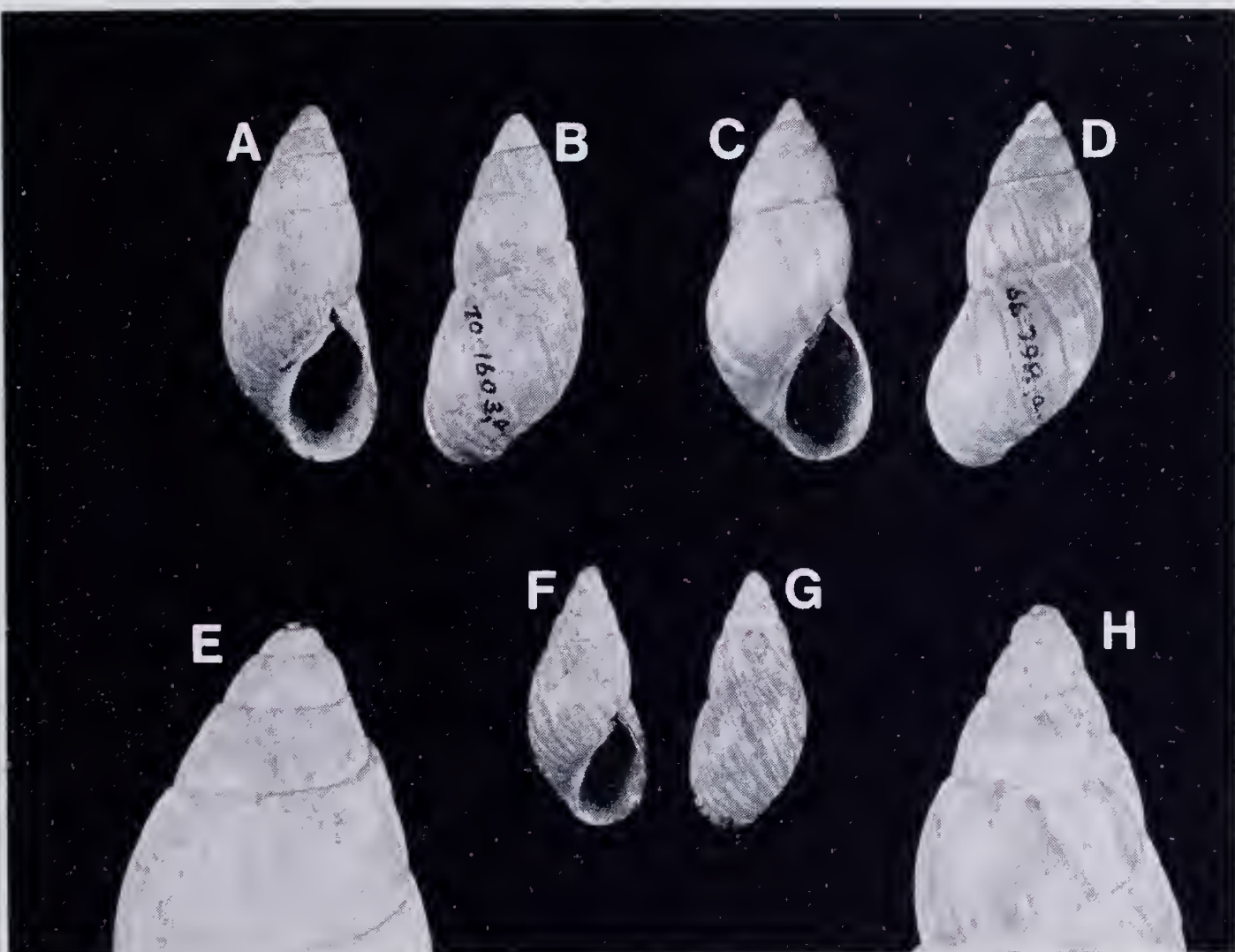


Figure 4.—*Bothriembryon gardneri* sp. nov. A, B, E.—Holotype, WAM 70.1603a C.-D.—Paratype 66.798a. *Bothriembryon consors* sp. nov. F.-H.—Holotype, 72.421a E. and H. x 3; all others x 1.

shell filled with brown calcarenite; 65.33, 2 shells; 65.34, 3 shells; 65.480, 1 shell; 70.900, 10 shells; 72.420, 32 shells; 73.253, 1 deformed shell, probably of this species; 73.254, 1 shell; 75.860, 2 shells; 9881, 2 shells in brown calcarenite: FMNH 182298, 7 shells.

Type locality. Point d'Entrecasteaux, Western Australia. Shallow quarry on crest of low ridge of calcarenite on north side of track from Windy Harbour to Salmon Beach. The site is located 3.5 km on a bearing of 32° from the Point d'Entrecasteaux lighthouse. Lat. $34^\circ 49' 14''$ S, long. $116^\circ 00' 52''$ E (Fig. 5).

Diagnosis. A large, robust *Bothriembryon*, elongate-ovate, up to 45 mm high, with a height usually greater than twice the maximum diameter and spire height more than half the total height. Whorls convex, about 5.7 in a height of 40 mm, sculpture of strong, colabral growth rugae, generally without spiral granulation. Protoconch of 2.1-2.3 slightly convex whorls, dome-shaped; sculpture fine, mainly reticulate over the first 1.5 whorls and tending to become axially aligned or wrinkled over the abapical portion, where weak axial rugae may also dev-

elop. Traces of whitish axial flames are sometimes apparent on the abapical portion of the protoconch.

Description of holotype. Shell large, robust, of 6 whorls in a height of 43.5 mm, maximum diameter 19.5 mm, height of spire 24 mm. Whorls convex, suture impressed and lightly crenulated; sculpture of colabral growth rugae, concentrated below the suture; spiral sculpture absent. Umbilical fissure small. Parietal callus thick, columella concave, thick and reflected. Protoconch dome-shaped, of 2.1 whorls, bearing a fine axially-reticulate sculpture, which becomes progressively more axial on the abapical portion, where weak axial rugae, anticipating the teleoconch sculpture, also appear. The cavity of the shell contains a friable, cream calcarenite.

Observations. Of the described species of *Bothriembryon* from Western Australia (Iredale 1939), *B. gardneri* most resembles *B. fuscus* Thiele from the south coastal Karri forests between Torbay and Walpole. In the shape, size and sculpture of the protoconch, the two species are quite similar; furthermore in each a weak axial flame pattern can be detected occasionally

on the abapical extremity of the protoconch. The two species differ essentially in features of the teleoconch. The fossil species has a rather more elongate shell than *fuscus*; though attaining a slightly greater height than the living species (45 mm against 43 mm), *gardneri* does not reach the maximum width of *fuscus* (19.5 mm against 21 mm). The spire height of mature shells of *gardneri* invariably exceeds the aperture height, whereas in *fuscus* these dimensions are about equal, as Iredale noted. In details of the sculpture, the two species also differ. Axial growth rugae are much stronger in *gardneri* and spiral granulation is generally absent; traces of this feature may be detected under magnification on an occasional shell. Fine spiral granulation and (sometimes) striation ornament the spire whorls of *fuscus*. These occur on the shell proper and are not mere periostracal features. A Field Museum paratype from the Pt. d'Entrecasteaux cliff near the lighthouse shows traces of a wide, axial flame pattern on the teleoconch, such as occurs on some shells of *fuscus*.

This comparison of *B. gardneri* and *B. fuscus* shows that the two share a range of common characters and probably are closely related. Possibly the former stands in an ancestral position to the latter. If so, then the direction of morphologic change has tended toward a shorter, more ovate shell with fine spiral granulation in lieu of strong axial rugae. The presumably non-adaptive protoconch characters have remained unaltered over this time.

Fossil snails associated with *B. gardneri* include two congeners, one of which, *B. consors* sp. nov., is described below, as well as species of *Paralaoma*, and *Magilaoma* (Punctidae), *Pernagera* and one other charopid (Charopidae) and an undescribed assimineid (A. Solem, pers. comm., Sept. 1976). This assemblage suggests a humid, well-vegetated, probably forested environment at Point d'Entrecasteaux at the time of deposition, in contrast to the exposed coastal heath that presently characterises the area.

The species is named after Mr. G. Gardner of Northcliffe, who introduced the author to the type locality and assisted in the collection of the type material.

Geographic range. *Bothriembryon gardneri* is known only from the type and adjacent localities at Point d'Entrecasteaux, within 4 km of the lighthouse (Fig. 5). The material has been collected from natural and man-made exposures of fossil soils occurring on and beneath the surface of an elevated ridge of aeolian calcarenite, now truncated by a prominent sea cliff.

Stratigraphic range. No direct evidence of age for the calcarenite deposits at Point d'Entrecasteaux is available but, by analogy with similar formations in south-western Australia (Lowry 1967), a Pleistocene age is assumed. The uppermost fossil soil, containing abundant land snail shells, is generally well lithified and underlies a thin, brown, surface (possibly deflated) quartz sand. A Pleistocene age for the fossils appears probable.

***Bothriembryon consors* sp. nov.**
(Fig. 4, F, H)

Material. Holotype WAM 72.421a. Paratypes WAM 72.421b to e, j and k, 6 shells; 70.901a and b, 2 shells; 70.1602d, 1 shell. Other reference material WAM 70.1602a to c, e to g, i to m, o to q, 14 shells.

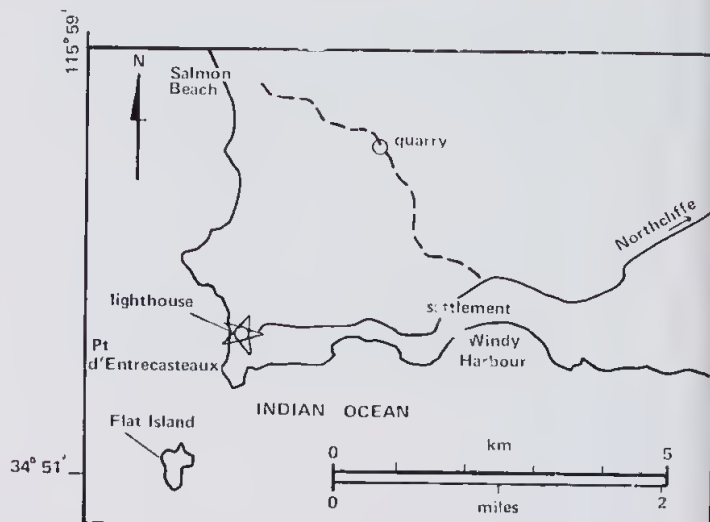


Figure 5.—Point d'Entrecasteaux and Windy Harbour. Quarry is type locality of *Bothriembryon gardneri* and *B. consors*.

Type locality. Windy Harbour, Western Australia. Shallow quarry NE of lighthouse beside track to Salmon Beach. The site is located 3.5 km on a bearing of 32° from the Point d'Entrecasteaux lighthouse. Lat. $34^\circ 49' 14''$ S, long. $116^\circ 00' 52''$ E (Fig. 5). This is the same place as the type locality of *Bothriembryon gardneri*, cited above.

Diagnosis. A medium-sized, robust *Bothriembryon*, elongate, up to 32 mm high, with a height about 2.1 times the maximum diameter; spire height slightly more than half the total height. Whorls gently convex, about 5.5 in a height of 30 mm; sculpture of fine, close, colabral growth lines crossed by fine spiral granulation, concentrated below the suture and becoming obsolete on the last whorl. Traces of narrow, brown and white axial striping are visible on some shells. Protoconch of 1.9 to 2.2 whorls, elevated, somewhat tumid, sculpture finely punctate with or without a weak axial alignment and becoming very finely axially wrinkled on the abapical extremity; pale axial flames present on the second whorl.

Description of holotype. Shell medium-sized, elongate, of 5.3 whorls in a height of 29.9 mm, maximum diameter 13.8 mm, height of spire 16.0 mm. Whorls gently convex, suture impressed and finely crenulated; sculpture of fine, close, colabral growth lines crossed by fine spiral granulation, concentrated below the suture and becoming obsolete on the last whorl. Columella slightly concave and reflected over a minute umbilical fissure. The teleoconch retains faded, narrow, brown and white axial striping. Protoconch elevated, slightly tumid, of 2.1 convex whorls bearing fine reticulate-punctate sculpture, which becomes axially wrinkled near the

abapical extremity; pale axial flames present on the second whorl. The cavity of the shell contains a friable, cream calcarenite.

Observations. From the combination of an attenuate shell, axially striped and with weak spiral granulation and a protoconch patterned with axial flames, it appears that the affinities of *Bothriembryon consors* lie with a group of species from south coastal districts typified by *B. kingii* (Gray). Shells of this general form occur from the vicinity of East Mt Barren westward to the Meerup River some 20 km north of Point d'Entrecasteaux, being represented by the species *marxwelli* Kobelt, *jacksoni* Iredale, *notatus* Iredale as well as *kingii*. The field relationships and precise differentiation of these species await clarification but examination of a range of recently collected material in the Western Australian Museum suggests that there is much intergradation in shell characters. Whether they represent one wide-ranging, variable species or several has yet to be demonstrated conclusively, but despite a generalised resemblance, the fossil species, *consors*, does not closely correspond to shells from any part of this series. Such similarities as can be seen are more noticeable with the attenuate shells that occur from Albany eastward and least of all with the wide, ovate shells that characterise the western end of the series.

In the ratio of height to maximum diameter, *consors* resembles shells of the type population of *B. kingii* from Albany, but differs in other characters. The fossil attains 5.5 whorls in a height of 30 mm, whereas *kingii* reaches only about 22 mm for this degree of coiling. The protoconch of *consors* is larger, more tumid, more finely sculptured and shows less axial alignment of the sculpture than typical *kingii*. Shells of *B. jacksoni* from the Walpole-Nornalup National Park are relatively wide with a height: maximum diameter ratio of 1.8:1, attaining 5.5 whorls in 27 mm; protoconch sculpture tends to be closer to that of *consors* than *kingii* but the teleoconch characters diverge markedly. Throughout the entire modern *kingii* series, the shells tend to be thin and fragile, even where obtained from calcareous coastal soils. By contrast, the shells of *consors* are all robust, some exceptionally so. This contrast between the two species applies to specimens from similar substrates and may represent more than a simple edaphic response. The differences in shell characters between *consors* and the modern *kingii* series (*sensu lato*) indicate that the group has undergone some morphologic divergence during the Quaternary. This may have been greater in the western part of the range, with the development of a wider, ovate form of shell. An overall trend within the group seems to have been the evolution of a relatively thin shell.

B. gardneri and *B. consors* contrast strongly in characters of the teleoconch. The former and larger species has about 5.7 whorls in a height of 40 mm, the latter about 5.5 spirally granose whorls in only 30 mm. The protoconchs of the two species differ in the number of whorls, degree of elevation, sculpture and pattern.

Geographic range. *Bothriembryon consors* is known only from the type and adjacent localities at Windy Harbour (= Point d'Entrecasteaux) within 4 km of the lighthouse (Fig. 5). The localities parallel those for *B. gardneri*, both species occurring together in the same fossil soils at Point d'Entrecasteaux. The name *consors* alludes to this association.

Stratigraphic range. As for *B. gardneri*, probably Pleistocene.

Bothriembryon douglasi sp. nov.

(Fig. 6, A-E)

Material. Holotype WAM 66.1036a. Paratypes WAM 66.1036b, c, 2 shells; 68.1434c, d, g, j and o, 5 shells. Other reference material, WAM 66.1036d to f, 3 shells; 68.1434a, b, e, f, h, i, k to n, 10 shells.

Type locality. Sea cliff at the Carrarang-Tamala boundary fence, Edel Land, Shark Bay, Western Australia. Lat. 26° 32' 26" S, long. 113° 26' 42" E; from within the top 7.5 m of the cliff (Fig. 7).

Diagnosis. A large *Bothriembryon*, ovate-conical, up to 35 mm high, height about 1.7 times the maximum diameter and attaining about 5.5 whorls in a height of 27 mm. Spire about half the total height or less; sculpture of fine, irregular growth lines crossed above the periphery by weak spiral granulation. Columella thin; umbilicus small, open. Protoconch bluntly rounded, of 2.1 to 2.4 wide, convex whorls, sculptured with fine, close irregular axial wrinkles. Protoconch apparently of one colour, slightly darker than the teleoconch.

Description of holotype. Shell large, ovate-conical, of 6.0 whorls in a height of 34.2 mm, maximum diameter 19.6 mm, height of spire 17.0 mm. Whorls convex, suture impressed and edged with a weak groove, base evenly rounded; sculpture of growth lines crossed above the periphery with fine, spiral granulation. Columella thin, reflected, partly obscured by matrix; umbilicus small. Protoconch of 2.1 whorls, rather worn but retaining traces of fine, close axial wrinkling; slightly darker than the teleoconch. The type is a dull-white, somewhat worn shell, cracked on the spire and lacking small sections of the outer layer in several places; the exterior carries some thin, pale-brown calcrete and the cavity is filled with a hard, pale-brown quartzose calcarenite.

Observations. In the form of the teleoconch and the sculpture and deeper shading of the protoconch, only one species, *B. distinctus* Iredale from the Balladonia district (Iredale 1939) shows any significant resemblance to *B. douglasi*. The similarity is less obvious with larger fossils, such as the type of *douglasi*, but more so with smaller shells, such as those from the "Zuytdorp" locality (Fig. 7), which are about the same size as mature specimens of *distinctus*. Spiral granulation on the teleoconch is a little stronger in *distinctus* and there is a size difference in the protoconch; that of *douglasi* ranges from 2.1 to 2.4 whorls, *distinctus* from 1.7 to 2.1 whorls. These differences, together

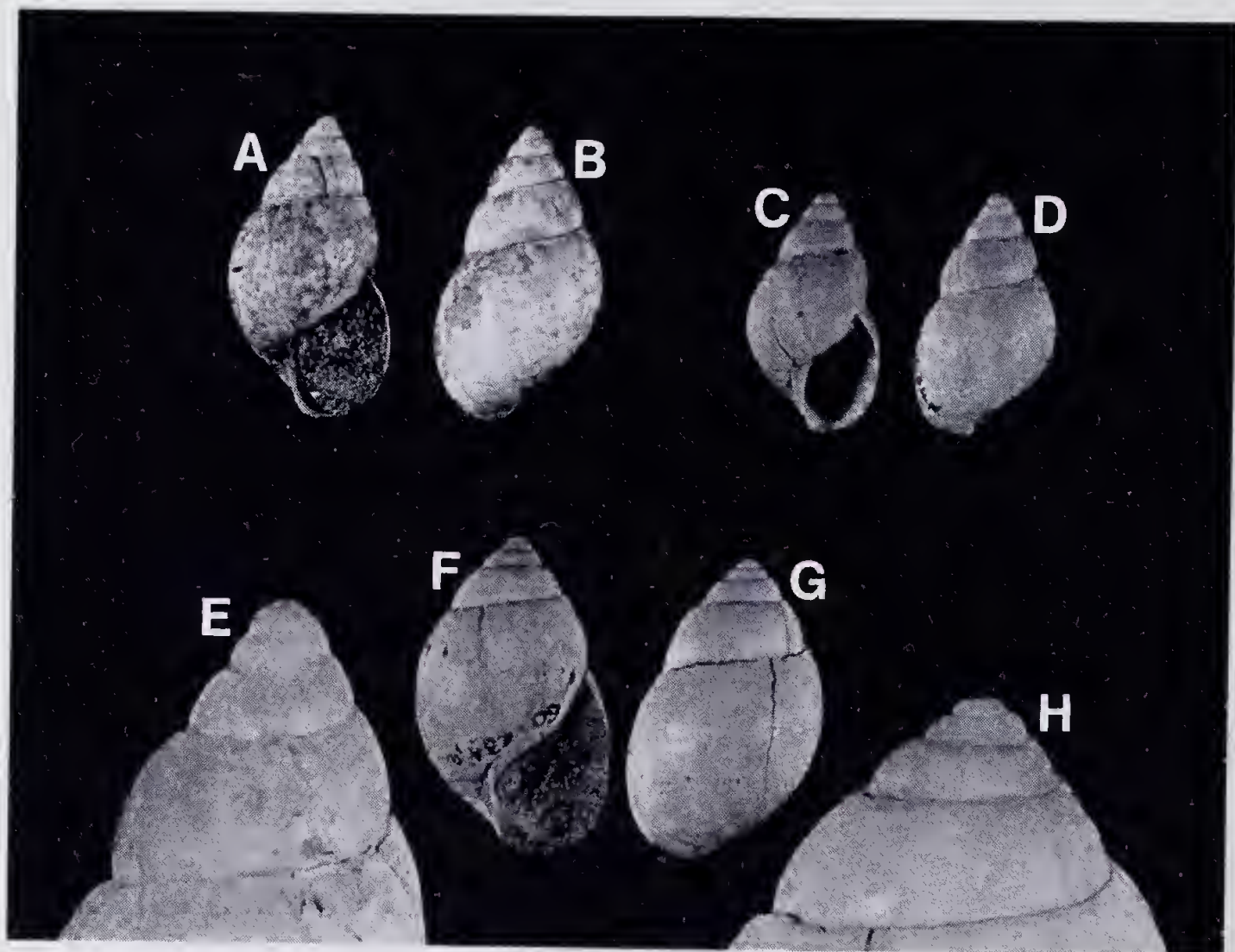


Figure 6.—*Bothriembryon douglasi* sp. nov. A,B.—Holotype, WAM 66.1036a. C–E.—Paratype 68.1434d. *Bothriembryon ridei* sp. nov. F,H.—Holotype, 60.434a. E and H x 3; all others x 1.

with the remoteness of the two geographic ranges (over 1000 km apart) suggest that the two species have been differentiated for an appreciable time.

At the type locality, the new species is associated with fossils of *B. costulatus* (Lamarck) (WAM 66.1037); a shell, probably also of Lamarck's species has been collected from a fossil soil at the "Zuytdorp" site (WAM 68.563) (Kendrick and Wilson 1975).

The new species is named after Mr. A. M. Douglas, who collected the specimens from the "Zuytdorp" locality, employed in this description.

Geographic range. *Bothriembryon douglasi* is known only from the type locality and from a similar position on the coastal cliffs at the site of the "Zuytdorp" wreck, 70 km further south.

Stratigraphic range. At both of the known localities, shells of *B. douglasi* occur in fossil soils similar to the Depuch Formation of the Shark Bay district (Logan *et al.* 1970). Specimens are associated with brown, quartzose, calcarenites; some from the type locality also bear

thin, hard crusts of light brown calcrete. A Pleistocene age seems probable for these lithified fossil soils.

***Bothriembryon ridei* sp. nov.**
(Fig. 6, F, H)

Material. Holotype WAM 60.434a. Paratypes WAM 60.434b, d, e, 3 shells; 66.660a, 74.531a. Other reference material WAM 60.434c, e to p, 13 shells; 65.1158, 1 shell; 66.660b to l, 11 shells; 66.675, 1 shell; 69.1207a to d, 4 shells; 70.1869a, b, 2 shells; 74.531b to h, 7 shells.

Type locality. Western side of Dorre Island, Western Australia; limestone cliffs opposite Disaster Cove. Lat. 24° 59' 52" S, long. 113° 07' 12" E (Fig. 7).

Diagnosis. A large *Bothriembryon*, ovate-conical, ventricose, up to 40 mm high, height about 1.5 times the maximum diameter and attaining about 6 whorls in a height of 38 mm. Spire less than half the total height; sculpture of fine growth lines with weak spiral granulation present above the periphery but becoming obsolete on the last whorl. Columella thin, umbilicus small. Protoconch of 1.8 to 2.1 whorls,

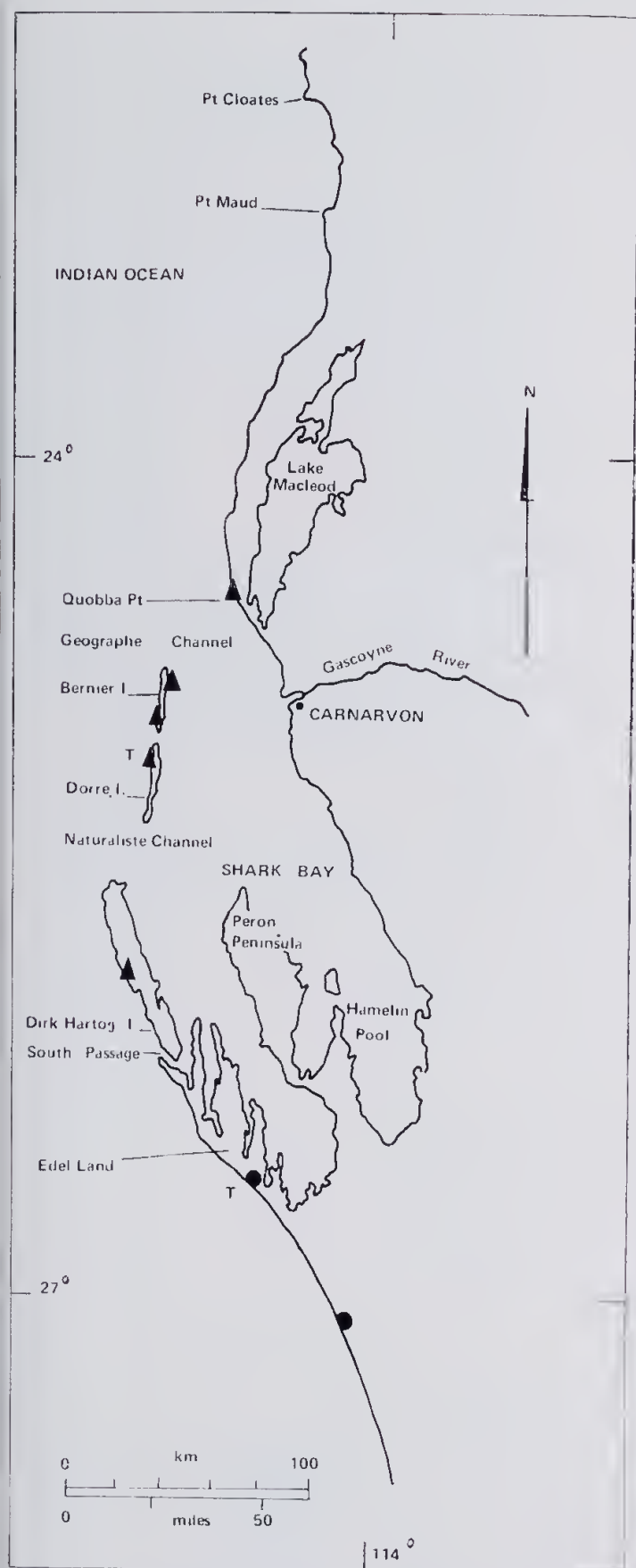


Figure 7.—Shark Bay district. *Bothriembryon douglasi* localities. ● *Bothriembryon ridei* localities. Δ Type localities T.

low and wide, sculptured with axial reticulation. Protoconch apparently of one colour, tending to be darker than the teleoconch.

Description of holotype. Shell large, ovate-conical, ventricose, of 5.9 whorls in a height of 36.3 mm, maximum diameter 22.7 mm, height of spire 16.0 mm. Whorls convex, suture impressed; sculpture of fine growth lines crossed by weak spiral granulation above the periphery and becoming obsolete on the last whorl; base evenly rounded. Columella thin, reflected; umbilicus filled with sediment. Protoconch of 2.0 whorls, low, wide, sculpture axially reticulate and strong; of one colour, slightly darker than the teleoconch. Like all the material to hand, the type is a dull white shell lacking other indication of the original colour. It is cracked in several places and part of the outer lip is missing. The cavity is filled with brown calcarete.

Observations. In form and size, *B. ridei* most resembles shells of *B. dux* (Pfeiffer), from the south coast region of Western Australia between about Ongerup and Caiguna. The new species however has a more ventricose shell, on which the spiral granulation is stronger and does not attain the height of the other (41 mm compared with 55 mm for *dux*). The protoconchs of the two species are of similar size but that of *ridei* exhibits a stronger axial component in the sculpture, best exemplified by paratype 60.434e.

The new species is named after Dr W. D. L. Ride, who, whilst Director of the Western Australian Museum, collected the type series and other material of this species.

Geographic range. Occurrences of shells of the present species at the type locality are discussed by Ride (1962, p. 24, 25, pl. 11). Additional occurrences are: Western side of Dirk Hartog Island, 32 km north of the homestead, apparently weathered from the cliff; Bernier Island, eastern coast near Wedge Rock and western coast opposite Red Cliff Point; Quobba Point near "The Blowhole".

Stratigraphic range. The report of Ride (1962) and field data recorded on labels accompanying the above material indicate that *B. ridei* occurs in fossil soils resembling those of the Depuch Formation, overlying the Tamala Eolianite. (Logan *et al.*, 1970). All specimens to hand are associated either with a dense, brown calcarete or indurated quartzose calcarenite. A Pleistocene age seems probable.

Late Quaternary climate in the Shark Bay district.

A comparison of modern and (what is known of) fossil land snail distributions in the Shark Bay district reveals some apparent contrasts which deserve consideration. Assuming that *B. douglasi* and *B. ridei* were broadly contemporaneous, it would appear that, at some as yet undefined stage of the Pleistocene, three species of *Bothriembryon*, all relatively large-shelled, inhabited the district; *ridei* occurred across western and northern Shark Bay and *douglasi* occupied the Edel Land coast (Fig. 7). The

distributions of these two species seem to have been allopatric. The third species, *costulatus*, which is extant (Kendrick and Wilson 1975), coexisted with both fossil species but the shells tended to be larger than modern specimens. The largest known example of *costulatus* (WAM 66.1037g, 6.2 whorls in a height of 30.1 mm) is a fossil from the type locality of *douglasi*. The extinction of two of these species and the size-reduction of the third presumably resulted from adverse environmental change, probably increased aridity. Whether this size-reduction applied generally to *costulatus* throughout its range, or featured local extinction and subsequent replacement by selected morphs of reduced size from outside the immediate area, remains speculative. The latter hypothesis is supported by the presence of distinctive, large-shelled populations of *costulatus* inhabiting the littoral fringe between Point Cloates and Point Maud. A shell of this form, from near the northern end of the species' range, was illustrated by Kendrick and Wilson (1975, Pl. IV, Fig. 11).

The Camaenidae, which incorporates the Chloritidae, Xanthomelontidae and Rhagadidae of Iredale (1939), are the principal family of land snails in arid Western Australia from Shark Bay northward, being particularly well developed in the Kimberley region (Wilson and

Smith 1975). At least four species represent the family in the Shark Bay district; one in particular, *Rhagada torulus* (Ferussac), is common on Bernier and Dorre Island and also occurs on Dirk Hartog Island and at Quobba and elsewhere on the mainland coast. Species of *Angasella* and *Plectorhagada* occur along the southern and south-eastern littoral and hinterland, while a *Plectorhagada* is present on Dorre Island. This group of snails is currently being studied by Dr A. Solem. Camaenid records are rare in west-coastal districts south of about latitude 27°, the peripheral occurrences in this region being *Angasella abstans* in the lower Murchison and Greenough districts (Iredale 1939 and G.W.K. unpublished notes). *A. abstans* appears to be a relict species with a strongly disjunct distribution, isolated from the main occurrences of the family. It may represent an earlier Pleistocene camaenid incursion into the northern fringe of the humid south-west. The family is absent from the south-western corner of the State, where *Bothriembryon* dominates the land-snail fauna.

No camaenid fossils have been found in association with either *B. douglasi* or *B. ridei*, despite the abundance of modern specimens, notably those of *Rhagada torulus*, at most of the known localities of the latter species (*ridei*). The few fossil records of camaenids from the

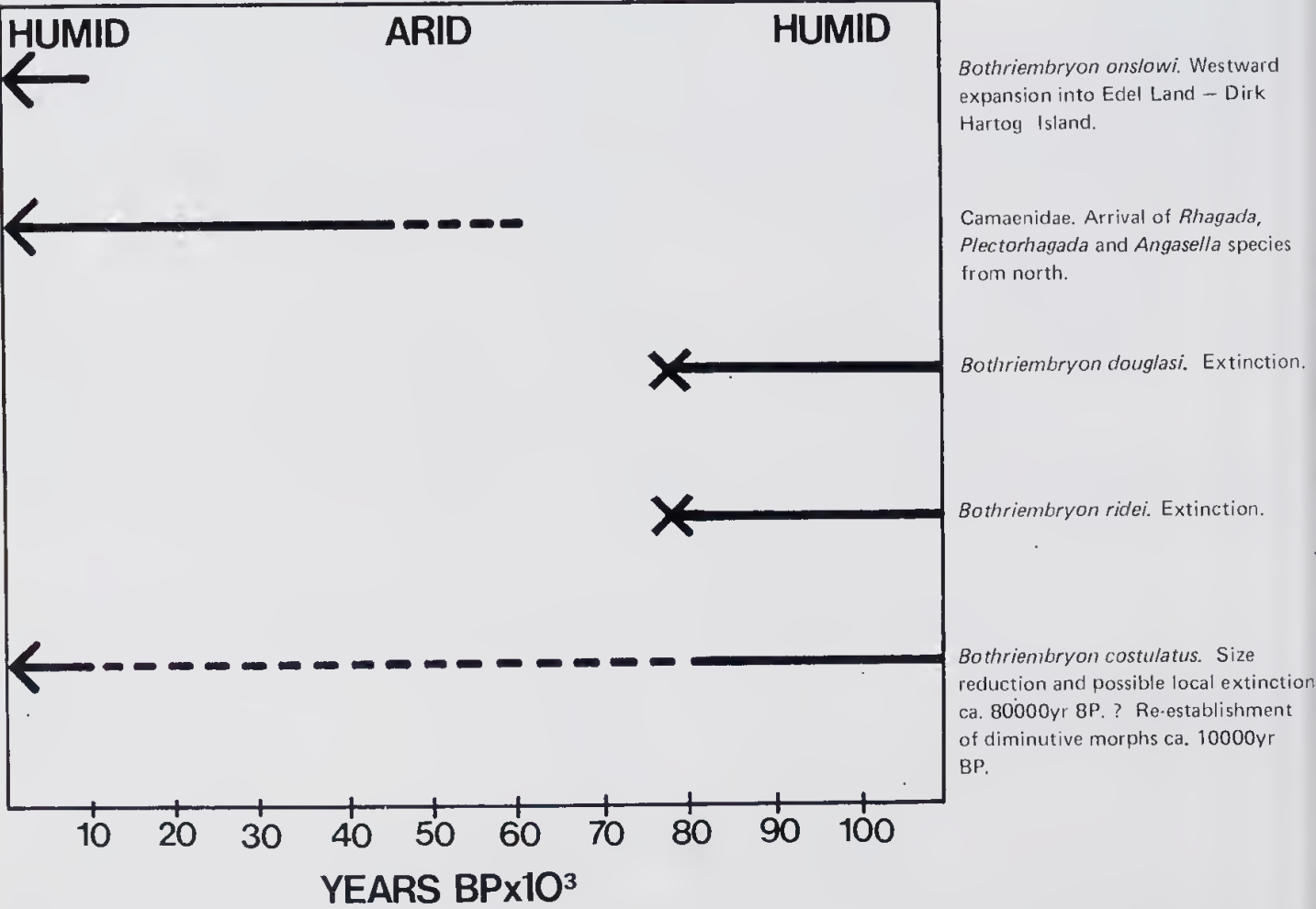


Figure 8.—Conjectural late Quaternary history of *Bothriembryon* and camaenid species in the Shark Bay District.

Shark Bay district (WAM 66.807, 73.85, 73.87) all appear to be of very recent geologic age. Significantly, all are associated with the diminutive, modern form of *Bothriembryon costulatus*, for which Iredale (1939) employed the name *B. minor* Pilsbry (Kendrick and Wilson 1975).

The evidence available from modern and fossil records suggests that the camaenid snails reached the Shark Bay district at some time after the extinction of *B. douglasi* and *B. ridei*. The demise of these two species and the size-reduction of *B. costulatus* are seen as consequences of an environmental change toward greater aridity. It is assumed that the camaenids, being pre-adapted to the drier conditions prevailing in northern areas, would have been favoured by any such change and would have extended their ranges southward and westward into the Shark Bay area. It is noteworthy that camaenids closely related to Shark Bay species are at present living in the country between the Gascoyne River and Cape Range; these may represent the original stocks from which the Shark Bay camaenid populations originated.

The timing of these events cannot yet be established precisely but some inferences can be drawn from the distribution data. Camaenid populations on Bernier and Dorre Islands have been isolated from the mainland since the submergence of the Naturaliste and Geographe Channels during the Flandrian transgression of the sea, some 8 000 year ago (Mörner 1971, p. 76). The bathymetry of South Passage between Dirk Hartog Island and the mainland indicates that severance of this island probably occurred a little later. Prior to this, the mainland connections of the Shark Bay "islands" would have been continuous for the entire duration of the last major glacio-eustatic regression of the sea, corresponding to the Wurm-Weichselian glaciation of northern Europe. During this period of global cooling, which became fully assertive from about 80 000 year ago (Broecker and van Donk 1970, Emiliani 1972), sea level fell more than 100 m below its present position (van Andel *et al.* 1967). The camaenid occupation of the Shark Bay district, in particular of the western islands, probably occurred during this time. If so, it may be assumed tentatively that the extinction of *Bothriembryon douglasi* and *B. ridei* marked a transition from (relatively) humid to arid conditions beginning around 80 000 year ago (Fig. 8).

Evidence in support of relative aridity in low and middle latitudes accompanying the reduced global temperatures of the last major glaciation of the Late Pleistocene has been advanced from studies in northern and eastern Australia (van Andel *et al.* 1967; Bowler and Hamada 1971; Dodson 1975), in south-east Asia (Verstappen 1974), the equatorial Pacific (Quinn 1971), tropical South America (van der Hammen 1972) and, in a review of all continents by Williams (1975), indicating a general convergence of views in this direction. Differences between modern and fossil distributions of land snails in the Shark Bay district are consistent with such an interpretation.

Still to be considered is the history of *B. onslowi* (Cox), the second extant species of *Bothriembryon* in the Shark Bay district (Kendrick and Wilson 1975). Fossils to hand are few (WAM 66.278, 66.658, 66.668, 71.225), all being derived from modern soil profiles of young geologic age. Associated fossils include the diminutive, modern form of *B. costulatus* but, as yet, no camaenids. The distribution of *onslowi* around southern Shark Bay, in Edel Land, on Peron Peninsula and Dirk Hartog Island (but not on Bernier or Dorre Islands) suggests that it entered the westernmost part of this range at a time when Dirk Hartog Island was joined to the mainland but when Bernier and Dorre Islands were not. As noted above, this would have been some time after 8 000 year ago. The living colours of *B. onslowi* are shades of a rather intense brown, matching the strongly coloured soils of Peron Peninsula and the south-eastern hinterland of Hamelin Pool. Well-developed cryptic coloration such as this supports the view that the species has had a relatively long association with areas of deeply coloured soils and a more recent presence in Edel Land and Dirk Hartog Island, where soils are pallid.

Acknowledgments.—I have to thank Mrs R. Roe of Beermullah for the collection of specimens and the provision of field data; and Mr G. Gardner of Northcliffe for assistance in the field and generous hospitality. Dr A. Solem kindly made available material from the collection of the Field Museum of Natural History and advised with the identification of associated fossil snails. Colleagues at the Western Australian Museum criticised the manuscript and suggested improvements. Maps were drawn by Ms P. M. Bradbury, and the photography done by Miss V. A. Ryland.

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Thallus variation in *Hormophysa triquetra* (C. Ag.) Kuetz. (Fucales, Phaeophyta) in oceanic and estuarine habitats

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Manuscript received 16 November 1976; accepted 22 February 1977.

Abstract

Hormophysa triquetra (C. Ag.) Kuetz. is one of the few fucoid algae which occur in Australian estuaries. There is a gradient of form variation between oceanic and estuarine environments. The morphological differences result from reduced cell enlargement and cell division in the estuarine compared with oceanic forms. However the pattern of growth and differentiation is the same in all forms so that delimitation of taxonomic sub-groups is not appropriate at this time.

Introduction

Several fucoid algae, including species of *Ascophyllum*, *Fucus*, *Hormosira* and *Pelvetia* penetrate into brackish waters, estuaries or salt marshes from rocky ocean shorelines in Europe, North America and New Zealand (Berquist 1959, Chapin 1976, Gibb 1967, South and Hill 1970). In these non-oceanic habitats the algae tend to have narrow fronds, few vesicles, profuse branching, no holdfast and no sexual reproduction. Low salinity has been suggested as the primary cause of these form changes, although Brinkhuis (1976) and Brinkhuis and Jones (1976) show that salt marsh ecads of *Ascophyllum* are the result of tidal emergence combined with high light and high temperatures. In addition, Moss (1971) suggests that the pattern of growth in *Ascophyllum* is irreversibly changed when vegetative regeneration of thalli occurs. In Australia however, the distributions and forms of fucoids in estuaries have not been documented or studied in relation to the environmental factors controlling growth in these habitats.

The wide form variation of *Hormophysa triquetra* (C. Ag.) Kuetzing has resulted in nomenclatural and taxonomic problems, but these have been resolved by Papenfuss (1967) and Womersley (1967). Some of these variations probably are estuarine forms of the species, but this distinction has not been made. Studies by Johnson (1967), Mairh and Krishnamurthy (1970) and Papenfuss (1967) have reported only on the vegetative and reproductive anatomy of the oceanic form of *H. triquetra*. The present study compares the vegetative morphological features of oceanic and estuarine forms of *H. triquetra* in Western Australia.

Material and methods

Material of *Hormophysa triquetra* was collected from the Western Australian coastline and voucher specimens were placed in the Herbarium of the University of Western Australia (UWA). Pieces of thalli from the extremes of the morphological ranges of estuarine (Peel Inlet) and oceanic (Cottesloe reef) environments were fixed in 6% formalin seawater or modified Karpechenko's solution. The tissue pieces were paraffin embedded. Transverse serial sections (4-9 μm) were stained with haematoxylin and mounted in Euparal. The morphologies of apical, mature and vesiculate tissue of oceanic and estuarine forms were compared by measuring tissue and cell (anticlinal and periclinal) dimensions, and by calculating the areas of the vesicular cavities. 160 cells were measured in each of 6 different thalli.

Results

Morphological variation

Although *Hormophysa triquetra* is a perennial species, it is vegetatively dormant and the fronds are denuded in winter. Growth occurs in spring and summer.

Oceanic forms: These forms occur in intertidal pools and in upper sublittoral areas of the limestone reef platforms of the southwestern Australian coast between Shark Bay (24°52'S; 113°39'E) and Fremantle (32°03'S; 115°45'E). The thallus (Fig. 1A) has triquetrous, twisted fleshy fronds with dentate, winged corners and embedded vesicles. Often, well developed lateral branches are difficult to distinguish from the main axis, resulting in a bushy habit. At north-

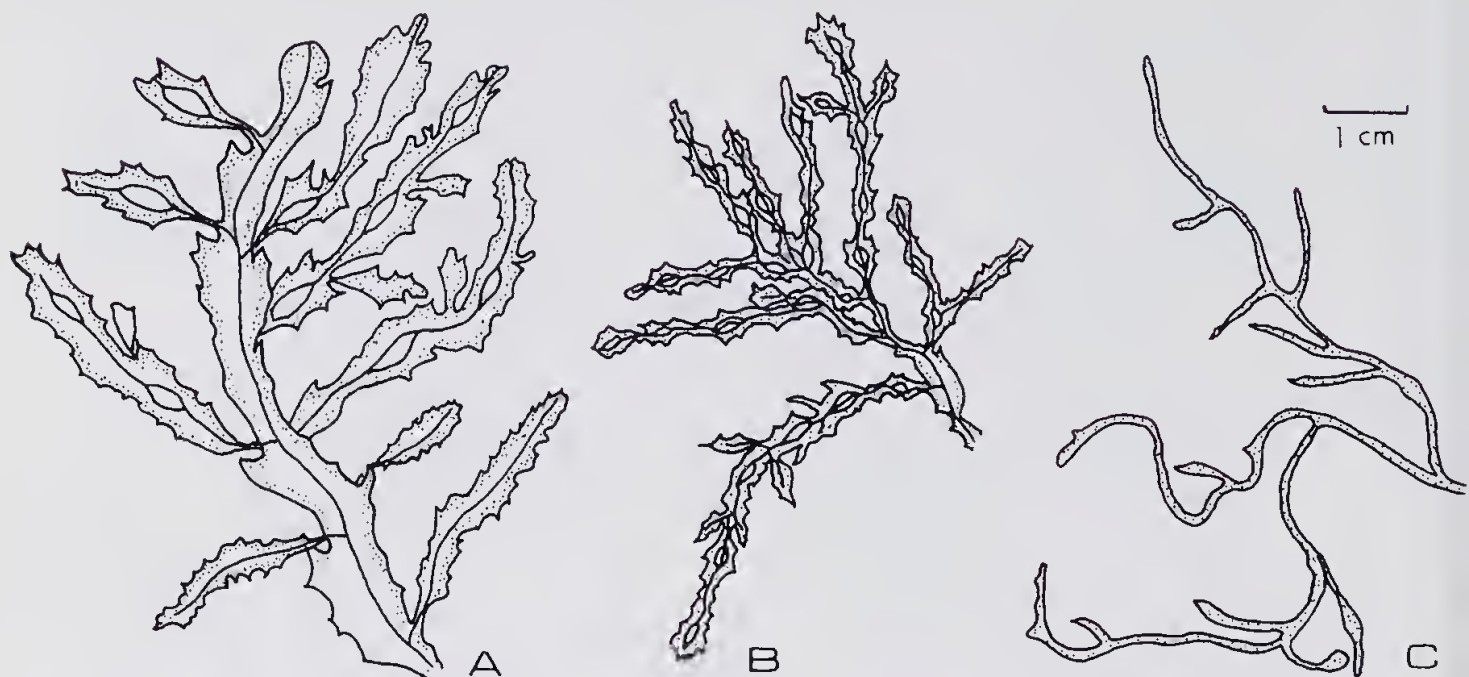


Figure 1.—A.—Portion of southern oceanic form of *Hormophysa triquetra* UWA-A1315. B.—Portion of northern oceanic form. UWA-A32. C.—Portion of estuarine form. UWA-A271.

erly locations, less fleshy specimens have been collected (Fig. 1B). Typical oceanic specimens are UWA-A1302, UWA-A1304, UWA-A1308, UWA-A1313 and UWA-A1315.

Estuarine forms: In the Swan River Estuary (32°03'S; 115°50'E) and Peel Inlet (32°35'S; 115°43'E), the alga grows subtidally to about 1.2 m depth. The thalli are usually attached by a holdfast to limestone rubble or to empty bivalve shells. In the most reduced forms, only portions of the lower thallus anchor the alga in the sandy substrate, or thalli without holdfasts are intertwined with the fronds of another estuarine fucoid, *Caulocystis uvifera*.

The morphology ranges from oceanic forms through reduced wing and narrow frond forms, to reduced spindly almost evesiculate forms. In the latter (Fig. 1C), frond parts near the apex are typically triquetrous, but with a tendency to become rounded lower in the thallus. The spindly forms have intertwining laterals and have a diffuse, entangled form. Typical estuarine specimens are UWA-A271, UWA-A372, UWA-A1037, UWA-A1291, UWA-A1295, UWA-A1298 and UWA-A1299.

Apical morphology

Cell divisions of the meristoderm and cortical layers built out from the faces of the tapered, triangular apical cell results in a triangular apex outline. The structure around the apical cell varies with habitat. Estuarine forms have three simple "horns" of tissue corresponding with the corners of the thallus outline. Thalli from the ocean reefs (Fig. 2A) have elaborate, tapering horns curved over the apical depression. The horns eventually contribute to the dentate wings of the mature thallus margin.

The spiral twisting of the fronds is initiated at the apex (Fig. 2B) because cells are cut off sequentially and slightly obliquely from the

apical cell. The spiral branching pattern from the corners of the triquetrous axis results from the successive initiation of lateral initials from the faces of the main apical cell. In oceanic forms (Fig. 2C), a wing of tissue overlies the entire young lateral branch. The basic spiral, monopodial growth pattern is the same in all forms of *Hormophysa triquetra*.

Mature frond and vesicle morphology

In both vesiculate and non-vesiculate areas of the mature fronds the oceanic form has larger cortical cells than the estuarine form (Fig. 3), although the dimensions of the meristoderm cells are similar in both forms. Conceptacular cavities occur in the oceanic form, but none occur in the most reduced of the estuarine forms.

Vesicles occur at irregular intervals along the fronds of both forms, but the estuarine forms have fewer vesicles. Increased cell division in the thallus surface layers ruptures the medulla and part of the inner cortex to form the vesicles cavity (Fig. 2D). The area of the vesicular cavities in the oceanic form ($\times 2.46 \text{ mm}^2$) is twice that of the vesicular cavities in the estuarine form ($\times 1.21 \text{ mm}^2$). The width of the vesicular cortex in the oceanic form ($\times 0.283 \text{ mm}$) is considerably thinner than in non-vesiculate areas of the thallus ($\times 0.388 \text{ mm}$), in contrast to the vesicular cortex of the estuarine form ($\times 0.199 \text{ mm}$) which is thicker than the non-vesicular cortex ($\times 0.153 \text{ mm}$). In both forms the inner cortex is distorted tangentially, and particularly in the oceanic form there is also rupture and loss of inner cortex cells. The

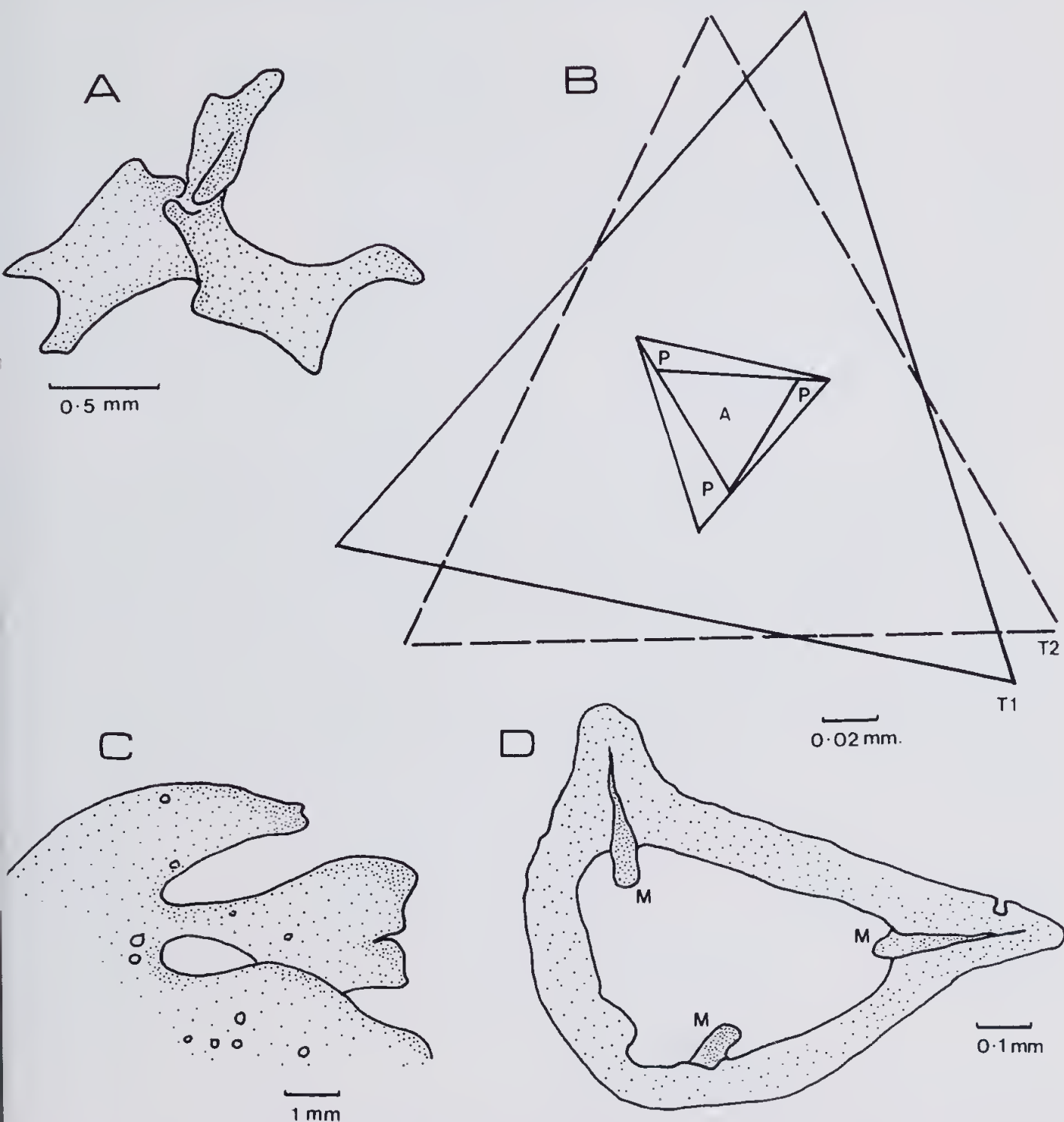


Figure 2.—A.—Top view of oceanic thallus apex of *Hormophysa triquetra* showing twisted horns over apical depression. B.—Diagrammatic outline of spiral apical growth pattern. A, apical cell; P, primary segments of apical cell division; T1 and T2, successive thallus outlines. C.—Oceanic form lateral branch apex with wing of parent thallus. D.—Transverse section of vesicle in estuarine form. M, remnant strands of medulla.

meristoderm and outer cortex cells have the same shape and size in both vesicular and non-vesicular areas since it is cell division in these tissues which forms the vesicles.

Discussion

The form variation of *Hormophysa triquetra* between oceanic and estuarine environments follows the same trend as reported for other fucoid species in similar environments. Perhaps

the same environmental factors cause similar types of morphological responses. As with other fucoids, the form variation of *H. triquetra* is a graded response suggesting that the factors controlling differentiation and form are quantitative rather than qualitative.

The morphological differences in *Ascophyllum* are attributed by Moss (1971) to fewer meristoderm cell divisions in reduced forms. In *Hormophysa triquetra* estuarine form, there are not

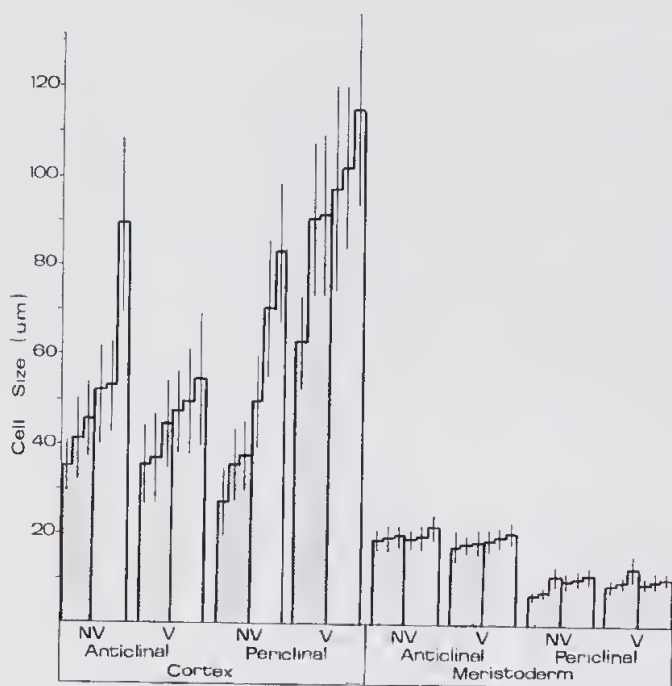


Figure 3.—Cell dimensions in vesiculate and non-vesiculate frond areas of three estuarine (shaded) and three oceanic thalli of *Hormophysa triquetra*. Anticlinal and periclinal indicate directions of cell measurement. V, vesiculate; NV, non-vesiculate. Standard deviation bars are shown.

only fewer meristoderm cell divisions as evidenced by the narrower frond and vesicle areas, but also smaller cortical cells. Although vesicle volumes were not compared because this study was based upon transverse sections of material, observations of longitudinal sections suggest that the above conclusions are applicable to this dimension as well. That is, the estuarine form differs from the oceanic form in its reduced cell enlargement and cell division capacities.

As for the taxonomic significance of the form variation in *Hormophysa triquetra*, there are several considerations. Firstly, the basic spiral growth pattern from a triangular apical cell, the pattern of initiation of laterals, and the

pattern of vesicle formation are the same in all forms. Secondly there are transition forms between the morphological extremes. Therefore there seems little merit in formalizing varieties or ecads of *H. triquetra* at this time, particularly without the support of eco-physiological data. Studies of variation in *Ascophyllum* by Brinkhuis and Jones (1976) and Brinkhuis, Temple and Jones (1976) suggest the directions for further study of *H. triquetra*.

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The soils, flora, vegetation and vertebrate fauna of Chatham Island, Western Australia

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Manuscript received 21 June 1977; accepted 21 June 1977

Abstract

The biological results of the first scientific survey of Chatham Island, of area 69 ha and maximum height 186 m, are presented. The two main soil types and two intermediate kinds are described. The island supports 46 vascular plant species (of which only 4 are alien), 4 species of lizards and breeding populations of the Little Penguin, Little and Flesh-footed Shearwaters, Welcome Swallow and Silvereye. A species of native rat occurs. The only known extant population in Western Australia of the fern *Asplenium obtusatum* occurs on the island.

Introduction

Between 11 and 22 May 1975 we visited Chatham Island in order to trap Silvereyes for genetic studies. Responsibility for the research carried out was as follows. Five mist-nets were operated for a total of 360 hours in a representative 4 ha area (IA) in which also a quantitative study of habitat structure and plant diversity was made (IA and JRW). Plant specimens were collected from this area as well as over the whole island and notes on the plant communities were made (IA). Soil profiles were dug at various sites and detailed descriptions were made (JRW). Several hours on two nights were spent noting seabirds coming ashore to roost (IA and JRW). This report presents annotated lists of the flora and vertebrate fauna, part of the quantitative vegetation survey, as well as an analysis of the soil types.

Physiography

Chatham Island (116°30'E, 35°02'S) lies west-southwest of Walpole, on the south coast of Western Australia, and has an area of 69 ha (calculated from aerial photograph). The land rises nearly perpendicularly from the sea to an elevation of 186 m near its southern end, and slopes gradually to the north. Seen from the east or west the island has a wedge-shaped appearance (Fig. 1). The island measures approximately 1.2 km by 1.0 km at its widest point. It lies 1.1 km from the mainland. The depth of the intervening strait is 37 to 63 m. The island was separated from the present mainland 11 000–12 000 years ago. To

the immediate east and south of the island depths range from 46 to 66 m (Admiralty Chart No. 1934 and D. Beale pers. comm. 1975).

The island is a granite-gneiss dome, of a type which is common in Western Australia. The resistance of such domes causes them to stand out as bosses often forming headlands, islands or peaks inland. On the southern side and near the summit very extensive areas of bare rock occur (Figs. 2, 3). A small area of limestone cliffs is present in the northwest corner. The average annual rainfall is probably similar to that of Walpole, and would be 1 400–1 500 mm.

Suitable landing sites are in bays on the north and west sides, but landing is difficult at all times owing to the swell. We landed in the northern bay.

History

The island was named Cape Chatham by G. Vancouver on 26 September 1791, after the Earl of Chatham. Vancouver's ship reached no closer than about 20 km and with poor visibility the island must have appeared as a conspicuous cape. Flinders in 1801 established its insular nature. William Nairne Clarke in his epic voyage from King George Sound to Nornalup and beyond in 1841 found Chatham Island on 6 March to be full of 'Sooty Petrel' burrows. He also found fur seals there.

The island has received little interference from man, although a fire was noted in the 1960s (D. Beale pers. comm. 1975). Small cairns at and near the summit show that the island has been landed on this century, probably by fishermen.



Figure 1.—View of Chatham Island from southwest.

Soils

There is only approximately 40% soil coverage on Chatham Island, most of the surface being bare rock. Thus, most of the soils are extremely shallow (0-40 cm) and overlie granite slabs and boulders. In the northeast sector, however, much deeper soils occur on the more gentle slopes and there has also been considerable movement of weathered parent material down-slope. This sector also exhibits marked differences in soil type due to the small outcrop of limestone (Fig. 2).

With the exception of isolated pockets, mainly near the summit of the island, all the soils have been extensively burrowed by seabirds to depths of up to 90 cm. The resulting soil disturbance and faunal wastes have clearly had a marked effect on soil formation.

The soils of Chatham Island were surveyed over a two day period, initially by two non-randomized transects across the major vegetation study area and later by a series of non-randomized soil pits located throughout the remainder of the island. Each profile examined was described *in situ* but pH, colour (Munsell soil colour chart) and texture were determined in the laboratory. A total of 15 soil pits and approximately 10 shallow inspection pits were examined. A generalized map of soil types is shown in Fig. 2.

Soils overlying granite

Peats.—Chatham Island experiences cool, wet conditions during most of the year due to its geographical location and highly exposed position. These climatic conditions have undoubtedly assisted in the development of shallow peats over most of the rock surface. In the deeper pockets of soil there is slight profile development (Appendix) and in some parts of the northeast sector there is clear evidence of ironpan formation, especially towards the limestone outcrops. The degree of *in situ* rock weathering within and to the base of soil profiles varies markedly from site to site and is generally associated with joints and discrete boulders.

Generally, the soils have a reddish-black surface horizon containing much organic matter and plant litter, and with an acidic pH in the range 4.0-5.0. In the deeper, more developed soils, there is a slight increase in fine clay with depth and overall a decrease in the amount of semi-decomposed plant litter. Feathers and other organic detritus occur in burrows at any depth and tend to complicate the rather subtle soil changes between horizons. There is usually a decrease in pH with depth to values as low as 3.5.

Many of these soils have poor drainage and the shallower soils in particular have a mass of plant roots and impeded lateral water movement at the soil/rock interface.

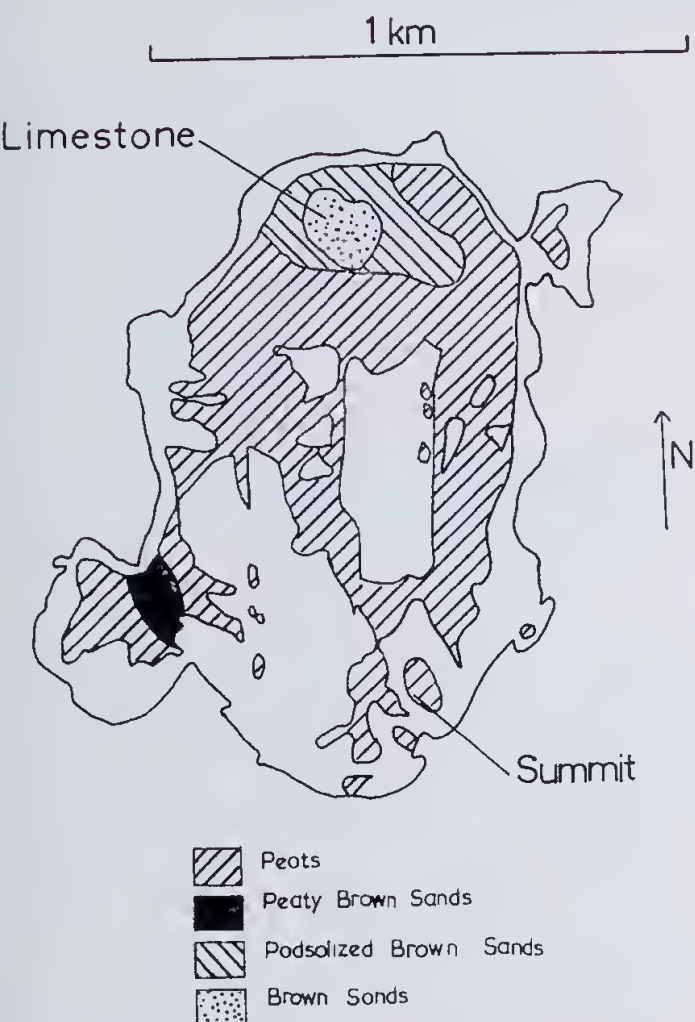


Figure 2.—The soils of Chatham Island. White areas represent (at this scale) bare rock.

Soils associated with limestone

Brown sands.—In the limestone area there are pockets of deep brown sandy soils occurring between exposed limestone outcrops. These soils show little horizon differentiation and are of neutral pH (6.5). Roots (*Rhagodia*) occur throughout the profile to depths of at least 60 cm but there is little surface accumulation of organic litter whether under *Poa* or *Rhagodia*.

Immediately downslope of the outcrops similar deep dark brown sands occur with a more marked brightening in colour (10 YR/4/6) at about 60 cm. These soils are alkaline (up to pH 7.9) with limestone fragments within the profile.

The brown sands are very freely drained.

Intermediate soils

Peaty brown sands.—This soil type occurs in a small area in the southwest sector, co-incident with the only area of *Atriplex* on the island (Fig. 3). It consists of a shallow brown sand (up to 60 cm) overlying granite, but with varying degrees of peaty surface horizon. Although there are no local outcrops of limestone, a large granite boulder nearby has remnant limestone attached to its underside. It

is possible that this soil is a relic deep brown sand originally developed from limestone but subsequently truncated and now supporting peat formation in the surface horizon.

Podsolized brown sands.—This soil occurs in a transitional zone between the main limestone outcrops and the granite exposures. It contains a purplish-black (5 RP/1.7/1) iron-rich zone with varying degrees of induration and iron pan formation towards the interface with a bright brown (7.5 YR/5/8) underlying sand. The pH of these two horizons is extremely low (3.2–3.4) despite the occasional presence of both granite and limestone boulders mainly in the upper part of the profile.

Flora

In the following annotated checklist of vascular plant species, the percentage frequency of plant species found in 50 randomly distributed quadrats in the 4.0 ha plot is indicated. An asterisk denotes naturalized alien species.

ADIANTACEAE

Cheilanthes tenuifolia (Burm.f.) Sw. (2%). Widespread on thin soil over granite slabs.

ASPLENIACEAE

Asplenium obtusatum Forst.f. Small clumps (<1 m² area) of this vigorously growing fern were found in only two places at the south end. The first was under boulders c. 180 m above sea level and the second was in a valley at the south end c. 100 m above sea level. This record is the second for the State. It appears that the first record (on Breaksea Island, 1866, where collected by G. Maxwell) refers to a population that is now extinct as IA specifically searched for the species there in August 1975. This species occurs also in New South Wales, Victoria and Tasmania, where it is not a rare species (Wakefield 1955).

POACEAE

Poa australis R.Br. (74%). See Fig. 3 for distribution.
Sporobolus virginicus (L.) Kunth.
**Ehrharta longiflora* Sm. (16%).
**Aira caryophylla* L.

CYPERACEAE

Carex preissii Nees. Found fruiting; only near sea level.
Scirpus nodosus Rothb.
Lepidosperma gladiatum Labill.

CENTROLEPIDACEAE

Centrolepis aff. *strigosa* (R.Br.) R. & S. Material is sterile. Rare; found on thin soil over granite slabs.

JUNCACEAE

Juncus pallidus R.Br. One clump only.

LILIACEAE

Chamaescilla corymbosa (R.Br.) F. Muell. (4%). Present as green fleshy projections from thin soil layer over granite.

ORCHIDACEAE

Cryptostylis ovata R.Br. Seen only in *Agonis marginata* and *Melaleuca microphylla* forest near summit.
Pterostylis vittata Lindl. Rare.

CHENOPODIACEAE

Rhagodia radiata Nees. See Fig. 3 for distribution. A few fruits noted.
Atriplex cinerea Poir. On west promontory only.
Threlkeldia diffusa R.Br. On limestone only.
Salicornia blackiana Ulbr. On west promontory only.

AIZOACEAE

Carpobrotus virescens (Haw.) Schwantes (8%). See Fig. 3 for distribution.

BRASSICACEAE

Lepidium foliosum Deav. Amongst *Poa* tussocks.

CRASSULACEAE

Crassula macrantha (Hook.) Diels (2%).

PITTOSPORACEAE

Sollya heterophylla Lindl. In flower.

GERANIACEAE

Pelargonium australe Willd. (2%). On thin soil over granite, usually with *Cheilanthes* and *Trachymene*.

**Geranium molle* L.

RUTACEAE

Boronia alata Sm.

Chorlaena quercifolia Erdl. (6%).

RHAMNACEAE

Spyridium globulosum (Labill.) Benth. Rare. A few bushes near south end.

DILLENIACEAE

Hibbertia cuneiformis (Labill.) Gilg. In flower.

MYRTACEAE

Agonis marginata (Labill.) Schau. One of two tree species on island. Flowers noted. See Fig. 3 for distribution.

A. flexuosa (Spreng.) Schau. Rarely exceeding 1.5 m in height probably owing to the exposed positions in which it grows. See Fig. 3 for distribution.

Melaleuca microphylla Sm. The rarer of two tree species on island.

Thryptomene saxicola (A. Cunn.) Schau (6%). Flowers noted. Widespread, particularly around granite slabs.

HALORAGACEAE

Haloragodendron racemosum (Labill.) Orchard. Very few flowers. See Fig. 3 for distribution.

APIACEAE

Apium prostratum Vent. Near sea-level.

Trachymene anisocarpa (Turcz.) Burtt (52%). Widespread through tussockland and on thin soil over granite.

EPACRIDACEAE

Leucopogon parviflorus (Andr.) Lindl. Seen only in valley at south end.

Andersonia sprengelioides R.Br. See Fig. 3 for distribution.

PRIMULACEAE

Samolus repens (Forst.) Pers. Near sea-level.

LOBELIACEAE

Lobelia alata Labill. Flowers noted. Near sea-level only.

ASTERACEAE

Olearia axillaris (DC.) F. Muell. ex Benth. A remarkable form in which the leaf shape and arrangement resemble those of *Westringia dampieri*.

Senecio lautus Forst. f. ex Willd. (4%). Near sea-level and throughout tussockland.

Calocephalus brownii (Cass.) F. Muell.

Actinobole uliginosum (A. Gray) Eichler. A few flowers noted.

Gnaphalium luteo-album L.

Helichrysum bracteatum var. *albidum* DC. A few flowers noted.

**Hypocheris glabra* L. One rosette found.

sp. indet. (seedling) possibly *Parietaria debilis* Forst. f. (10%).

sp. indet. (seedling) (2%).

sp. indet. (seedling) (2%).

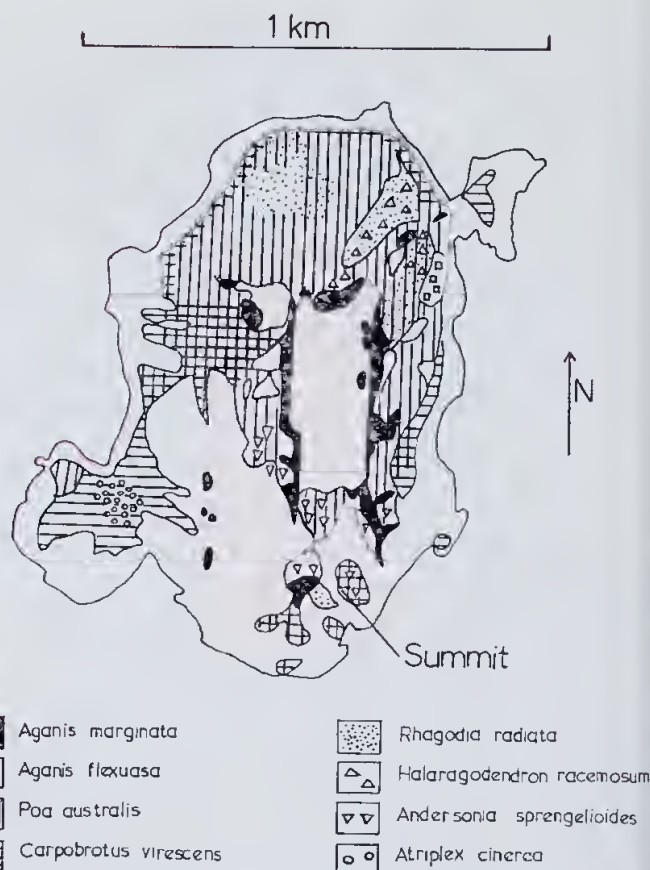


Figure 3.—Vegetation map of the island. White areas represent (at this scale) bare rock.

Vegetation

The main plant communities on Chatham Island are *Poa australis* tussock grassland, *Carpobrotus virescens* herbfield, *Rhagodia radiata* low closed-shrubland, *Agonis marginata* low closed-forest, and *Andersonia/Thryptomene/Cheilanthes* lithic complex. (See Fig. 3).

1. *Poa australis* tussock grassland. This community is the most extensive. Most cover is due to large tussocks (1 m high) of *Poa australis*, in between which *Trachymene*, *Senecio*, *Lepidium*, *Crassula*, *Ehrharta* and various small seedlings occur. On the western slopes of the island, especially at low altitudes, much *Carpobrotus* is present.

2. *Carpobrotus virescens* herbfield. This community is found on the two promontories and along the edges of the island. Near the summit *Carpobrotus* grows in windswept crevices containing very shallow soils. Associated genera are *Lobelia* (sea-level only), *Senecio*, *Sporobolus*, *Atriplex*, *Salicornia* (last two on west promontory only), *Samolus*, *Scirpus*, *Lepidosperma* and *Cheilanthes* (this last around rock slabs away from sea-level).

3. *Rhagodia radiata* low closed-shrubland. Near the limestone cliffs this species forms almost pure stands, with height not exceeding 1 m. Elsewhere *Haloragodendron* becomes codominant. In the valley at the south side *Apium*, *Boronia*, *Hibbertia*, *Chorlaena* and *Olearia*, amongst others, occur with *Rhagodia*.

4. *Agonis marginata* low closed-forest. Small stands of this species occur only in crevices with deep soil, where they are stunted. In valleys edged by near vertical granite slopes the species reaches 6 m. Considerable runoff must ensue from such places. Associated shrubs are *Melaleuca*, *Hibbertia*, *Chorilaena* and *Thryptomene*.

5. *Andersonia/Thryptomene/Cheilanthes* lithic complex. "Lithic" refers to the habitat of these plant species; they occur in thin layers of soil over granite or in small soil-filled joint lines in granite. On the plateau around the summit the first species occurs in cushion-like form and *Thryptomene* is a windblown bush no higher than 30 cm. *Thryptomene* occurs with *Cheilanthes* elsewhere around slabs of granite or on thin soils over granite over most of the island.

Vertebrate fauna

Amphibians

None were noted. Tadpoles were specifically searched for in the many pools of rainwater on the plateau leading to the summit.

Reptiles

Four species of lizards were noted. Snakes are absent.

Phyllodactylus marmoratus. Common under slabs of exfoliated granite.

Ctenotus labillardieri. One was found in soil under a *Poa* tussock.

Hemiergis peronii. Four were found under *Poa* tussocks.

Egernia kingii. The most abundant lizard species. It was found from sea level to summit excluding large expanses of rock devoid of pockets of vegetation or slabs. All specimens were black with prominent yellow markings.

Birds

Eudyptula minor, Little Penguin. Very common and found along all accessible parts of the coast (i.e. the north and west parts) in *Carpobrotus* and *Poa*. They were recorded as coming ashore 45 minutes after nightfall and leaving about 45 minutes before first light.

Diomedea melanophrys, Black-browed Albatross. Two were seen offshore near the west and north sides respectively.

Puffinus assimilis, Little Shearwater. Only a few were seen, above the campsite amongst *Poa* tussocks. Only one skull was found.

P. carneipes, Flesh-footed Shearwater. This presumably is the 'large Sooty Petrel' found on the island in 1841 by Nairne Clarke. For the time of the year, the birds were surprisingly common. On a walk around the northern parts of the island one night we saw one adult every 15-30 m. No chicks were seen but during the day noises from underground were attributed to this species. Dozens of skulls were picked up over the island.

Sula bassana, Gannet. Three followed the boat as we approached the island.

Ardea novaehollandiae, White-faced Heron. One, presumed vagrant, was seen most days around the island.

Haliaeetus leucogaster, White-breasted Sea-eagle. One pair was seen most days, but they were never seen perched. No nest was found.

?*Falco peregrinus*, Peregrine Falcon. On 21 May one bird was seen briefly near the northern end, and IA's field notes are 'One falcon with black head; larger than Kestrel but smaller than Brown Falcon'.

Falco cenchroides, Kestrel. One pair was present. One bird was seen perched on an inaccessible ledge once; no nests were found.

Haematopus fuliginosus, Sooty Oystercatcher. Foraged on the more gentle granite slopes leading into the sea. Usually two or three birds were visible from the campsite. The maximum number of birds seen together was five.

Larus novaehollandiae, Silver Gull. Occasionally present at the campsite. Maximum number seen was 20. There was no evidence of breeding.

Sterna bergii, Crested Tern. One was seen fishing off the landing place on 17 May.

Dacelo novaeguinae, Kookaburra. One bird, presumed vagrant, was heard and seen in *Agonis marginata* scrub on 19 May at an altitude of c. 100 m.

Hirundo neoxena, Welcome Swallow. Common. Maximum number of birds seen at one time was 35. Two old nests were found in a cave on western side of island. The very spacious cave on the eastern side, which is unfortunately inaccessible, probably contains many nests as Swallows were seen to fly in and out of the cave.

Petroica multicolor, Scarlet Robin. One male, presumed vagrant, was netted, banded and released on 12 May.

Zosterops gouldi, Silvereye. Common over the whole of the island, but mostly seen in *Rhagodia* bushes. However few fruits were available so the birds were probably mainly eating insects. One hundred and thirty-two feeding actions were recorded, distributed as follows: 68% on *Rhagodia* leaves, 23% on *Haloragodendron* leaves and 9% amongst foliage or flowers of *Agonis marginata*. Thirty-four birds were netted, banded and released. An old nest was found in an *Olearia* bush, 1 m from the ground, at an altitude of c. 100 m.

Mammals

Rattus fuscipes. These were common around the boulders near the campsite, but none were noticed elsewhere. Several drowned in a bucket of water and were donated to the Western Australian Museum.

No mice, rabbits, goats, macropods or seals were noted. Fur seals occurred on the island in the past (Nairne Clark 1841; Cumpston 1970, p. 91). Seals are occasionally recorded at Windy harbour, 50 km north-west of Chatham Island (D. Beale, pers. comm. 1975).

Discussion

Despite the shallow nature of the soils on Chatham Island some interesting aspects of soil formation can be observed. The dominant climatic influence is undoubtedly a cool moist condition prevailing for most of the year. This condition is due both to rapid surface runoff from bare rock surfaces on the island and to the exposed position of the island.

In general there is little correlation between vegetation boundaries and soil distribution. There would probably be better correlation on the mainland. On Chatham Island, virtually all soils are so disturbed by the burrowing habits of fauna that effects of vegetation on soil formation are minimized. Although no chemical analyses were performed on the soils it is predicted that their nutrient status will be relatively high due to excreta and other faunal wastes deposited in and around burrows.

The most recent and detailed soil survey close to Chatham Island is that of McArthur and Clifton (1975) in the Pemberton-Mt. Chudalup region, located about 30 km to the northwest on the mainland. The peats on the island are probably representative of the *Chudalup association*, whereas the other soils discussed clearly belong to the *d'Entrecasteaux association*.

The flora and vertebrate fauna of Chatham Island are certainly depauperate, but no exact figures can be given because the plants and animals occurring on the immediate adjacent mainland have not been documented. In view of the exposed nature of the island, the absence of eucalypts is not surprising. During the last glacial when sea-levels were 100 m lower than at present, Chatham Island would have been merely a prominent hill about 25 km from the ocean. At present Mt. Chudalup (185 m high) lies close behind Windy Harbour and the deep red loams around it support karri (*Eucalyptus diversicolor*) forest with its characteristic suite of plant species. Thus karri would conceivably have grown around Chatham Island on areas now covered by the sea. It is likely that Yate (*Eucalyptus cornuta*) and Bullich (*E. megacarpa*) occurred on the island.

The absence of various sea birds, in particular *Pterodroma macroptera* (Great-winged Petrel) and *Larus pacificus* (Pacific Gull) is remarkable. The absence of the former is interesting. On Eclipse Island (near Albany) in April 1975 (where two migratory seabirds, the Flesh-footed Shearwater and the Great-winged Petrel, occur) adult Shearwaters had ceased visiting the island. The Petrels had first arrived in March. On Chatham Island some adult Shearwaters were still visiting the island during May. On Sandy Island (50 km north-west of Chatham Island) Flesh-footed Shearwaters occur without *Pterodroma* and adults were noted by IA returning at night as late as April 1976. These facts seem to indicate a negative interaction, perhaps mediated through availability of burrowing space, between the two species on Eclipse Island.

The Cape Barren Goose, *Cereopsis novaehollandiae*, probably occurred on Chatham Island in the past as it formerly ranged as far west as Cape Leeuwin prior to the arrival of sealers and fishermen. Certainly the island appears suitable to support three or four pairs. It may be feasible to stock the island with several pairs from the Archipelago of the Recherche.

As Pied Cormorants are absent from the coastline near Chatham Island no trampling of the vegetation on the island is evident. Burrowing species of seabirds (Little Penguin, both Shearwater species) disturb the soil and manure it (Gillham 1963), and a peculiar vegetation pattern on the north side of the island may reflect past deleterious influences by the burrowing seabirds. Amongst the *Poa* tussockland there is a large strip of dead *Poa*, running from near sea-level to a height of c. 100 m. There was no evidence that this had resulted from fire.

Acknowledgements.—IA's research on genetical variation in Silvereyes is financed by a grant from the Australian Research Grants Committee. We also thank Messrs. Derrick and Barry Beale for transport; Dr M. J. Mulcahy and Professor A. M. Posner for useful comments on the soil descriptions; Dr N. G. Marchant for identifying or checking IA's identifications of plant species; Mr G. G. Smith for identifying the *Asplenium*; Dr J. H. Willis for information about Maxwell's collecting sites; Dr D. L. Serventy for information about Nairne Clarke; Dr D. Kitchener for identifying the *Rattus* and Dr G. M. Storr for identifying the lizards. We are also grateful to the W.A. Wildlife Authority for permission to work on Chatham Island.

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Appendix

Peat with profile development (Site No. 5)

Aspect: 330°.

Slope: 10°.

Height: 100 m.

Rock type: granite.

Vegetation: *Agonis marginata*, *Rhagodia*, *Boronia*, *Olearia*, *Chorilaena*, *Melaleuca microphylla*.

1. 0-2 cm Reddish black (7.5 R/1.7/1); loamy texture containing sand and plant litter; loose structure; gradual change to
2. 2-12 cm Reddish black (5 R/1.7/1); silty loam texture with sand grains; gradual change to
3. 12-25 cm Reddish black (2.5YR/1.7/1); sandy loam with occasional boulders; loose structure; gradual change to
4. 25-45 cm Dark reddish brown (7.5YR/3/2); indurated gravelly loam; gradual change to unweathered granite.
 - (a) pH 5.30 in horizon 1 with gradual increase to pH 5.55 in horizon 4.
 - (b) Increase in fine clay with depth.

The flora and fauna of Dirk Hartog Island, Western Australia

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Manuscript received 21 June 1977; accepted 26 July 1977

Abstract

Dirk Hartog Island (62 000 ha), which lies off Shark Bay, Western Australia, between 25°30'S and 26°15'S, has been visited and studied by a succession of visitors since 1616. It consists of Quaternary Tamala Eolianite which forms rugged cliffs along much of the coast. The rainfall averages 313 mm, falling mostly in winter, while average temperatures range from 11-21°C (winter) to 22-32°C (summer).

There are five vegetation types: tall open-heath; low closed/open-heath with hummock grasses; low very open-heath; hummock grassland; and low open-shrubland. The known indigenous flora totals 258 species in 167 genera of 67 families. Of the named species, 77 are South Western, 61 Eremean and 102 common to both. The island is floristically transitional between the South West and Eremean Botanical Provinces but with a leaning to the South West. Thirty six species, mostly of European origin, have become naturalised.

Two species of macropod marsupials, *Lagostrophus fasciatus* and *Bettongia lesueur*, once occurred on Dirk Hartog but are now extinct. Two species of rodents, *Pseudomys albocinereus* and *P. hermannsburgensis* are present although not previously reported. Cats, goats and the House Mouse have become feral. Some 84 species of birds have been recorded by a number of visitors over the years. Most have wide-ranging distributions but a few southern species occur here at or near the northern limit of their range. Of especial interest is the Black-and-white Wren (*Malurus leucopterus*) which is restricted to Dirk Hartog and Barrow Islands. Twenty-seven species of terrestrial reptiles have been collected. Most are typical of the warmer and drier parts of southern-Western Australia.

Introduction

Dirk Hartog Island, the westernmost part of Australia, is a large island of about 62 000 ha which encloses the western side of Shark Bay, Western Australia (Fig. 1).

The first recorded landing by a European in Australia is that of the Dutchman Dirk Hartog at Cape Inscription, the northern tip of the island, in 1616 (Flinders 1814). Other early visitors were Vlaming in 1697 (Flinders 1814), William Dampier in 1699 (Dampier 1729), the Audin expedition in 1801 (Péron 1807, Baudin 1874), Freycinet in 1818 (Quoy and Gaimard 1824), King and Cunningham in 1821 (King 1827) and Grey in 1839 (Grey 1841).

More recent visitors who have reported on aspects of the biology of the island include T. Carter in 1916 (Carter 1917) and 1922 (Carter 1923), F. Lawson Whitlock in 1918 and 1920 (Whitlock 1921), E. Ashby in 1927 (Ashby 1929), a group of students from Wesley College in 1967

(Sedgwick 1967, 1968), B. A. and A. G. Wells in 1973 (Wells and Wells 1974) and J. S. Beard in 1974 (Beard 1976). Most of the recent reports concentrate on birds and give only brief reference to other animals or plants. An exception is the description and map of the vegetation by Beard (Beard 1976).

Since 1899 Dirk Hartog Island has been held under pastoral lease as a sheep station. The whole island is leased except for 81 ha of freehold land and three small reserves at the northern tip containing the lighthouse and inscription posts (Reserve Nos. A12715, 14918 and 11634).

In 1972, the present lessee, Sir Thomas Wardle, invited the authors to visit the island and make an inspection.

The first visit took place from 2 to 8 September 1972. Personnel were A. S. George (Western Australian Herbarium) T. Evans and A. A. Burbidge (Western Australian Wildlife Research

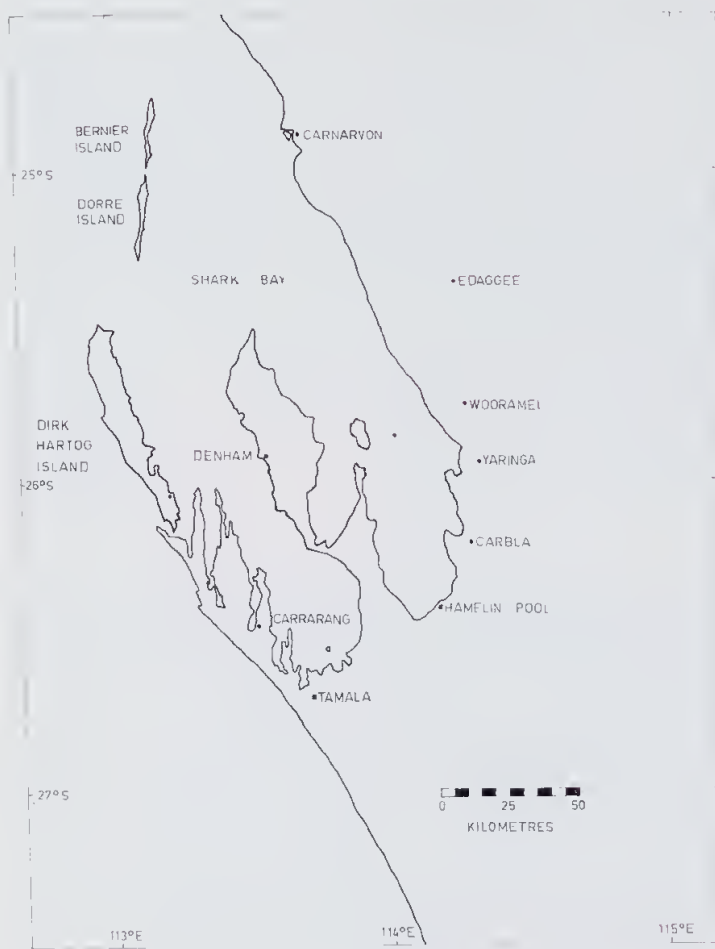


Figure 1.—Map of the Shark Bay area.

Centre). During this visit as much of the island as possible was traversed, using station tracks. In the daytime plants and animals were collected and observations were made on birds. Much time was spent searching for evidence of native mammals, such as tracks, droppings and skeletal remains. At dusk and after dark, spotlight traverses were carried out by vehicle and on foot. Traps were set for small mammals at various localities. The traps used were Elliott live traps (32 cm x 10 cm x 8 cm) and metal break-back traps.

Further visits which have been made to the island by staff of the Wildlife Research Centre have resulted in additional information. In April 1974 further small-mammal trapping and general collecting was carried out by W. K. Youngson.

Physical description

Dirk Hartog Island is about 79 km long and a maximum of 11 km wide with the long axis aligned 340°. The southern end (Cape Ransonnet) is separated from the mainland by South Passage which at its narrowest is about 2 km wide (Fig. 2).

Geologically the island is made up of Quaternary (probably Pleistocene) Tamala Eolianite (Logan *et al.* 1970). The geology of Bernier and

Dorre Islands and the Edel Peninsula is similar but Quaternary sandstone occurs on Peron Peninsula.

The western side of the island is bounded by steep cliffs which range in height from 2 or 3 m to about 80 m near Herald Heights. The eastern side has a few comparatively low cliffs with extensive sandy and rocky beaches in between. Sand dunes lie behind the beaches in places.

The western side of the island is the higher, rising to 185 m at Herald Heights and to 155 m and 132 m further north. The middle parts consist mainly of well-vegetated stable sand dunes of reddish or whitish calcareous soil although in the area between Herald Heights and Tetrodon Loop there are a number of mobile white dunes, one of which touches the sea at Tetrodon Loop. Near the cliffs the soil is shallow and the limestone frequently crops out. A number of low-lying areas contain clay pans.

Climatological data are given in Table 1. It can be seen that most rain falls during the winter but that occasional summer cyclones or thunderstorms also bring rain. The rainfall on Dirk Hartog is higher than that on the adjacent mainland; only Carrarang and Tamala Stations to the south approach the figure for Dirk Hartog. This is possibly an orographic effect since Herald Heights and the other hills along the west side of Dirk Hartog Island are the highest land for some distance.

There is no standing fresh water on the island except in clay pans for a short time following heavy rain. Water has been provided for the sheep from wells. At Herald Heights there is a seepage in a small cave just below the clifftop. Stalactites and associated features have formed, indicating that the water supply, though small, must be fairly constant. It was dripping freely at the time of our visit in 1972.

Vegetation and flora

Shark Bay is the site of the first authenticated botanical collections by Europeans in Australia. William Dampier, on his second visit there between 6 and 12 August 1699, collected at least 18 species which are now in the Sherardian Herbarium at Oxford University (George 1971). Although he landed on Dirk Hartog Island, we do not know which of his plants were collected there. Dampier's name is commemorated in the genus *Dampiera* and the species *Beaufortia dampieri*. Several other names commemorating him have unfortunately been reduced to synonymy, e.g. *Clianthus dampieri* (now *C. formosus*) and *Eurybia dampieri* (*Olearia axillaris*).

Later visitors who collected around Shark Bay included Leschenault, Riedle, Péron and Guichenot with Baudin in 1801 and 1803 (Baudin 1974), Gaudichaud, Quoy and Gaimard with Freycinet in 1818 (Gaudichaud 1826), Cunningham with King in 1822 (King 1827), Grey in 1839 (Grey 1841), Milne with Denham in 1858 and Mueller in 1877 (Mueller 1883). Not all landed on Dirk Hartog Island. Since

Table 1

Climatic data for Dirk Hartog Island and nearby locations, from information supplied by the Bureau of Meteorology.

Rainfall (in mm)				
Station		Mean	Median	Range
Dirk Hartog Homestead (1893-1948)				
January	6	0	0-89
February	12	4	0-135
March	13	2	0-130
April	16	7	0-74
May	56	47	0-299
June	88	88	7-222
July	62	50	17-202
August	35	29	4-122
September	14	8	0-61
October	7	5	0-40
November	2	0	0-11
December	2	0	0-34
Annual	313	290	120-681
Other Stations.				
Carrarang (1894-1973)	280	268	71-532
Tamala (1900-1975)	300	285	122-490
Denham (1893-1975)	236	223	78-522
Hamelin Pool (1885-1975)	213	194	45-409
Carbla (1913-1975)	216	190	63-446
Yaringa (1923-1975)	210	185	56-438
Wooramel (1898-1975)	201	184	60-472
Edagee (1915-1975)	192	175	61-447
Carnarvon (1883-1950)	229	205	68-619

Evaporation (in mm)	
Station	Annual average
Denham	2 032
Hamelin Pool	2 108
Carnarvon	2 465

Temperature (in °C).						
			Carnarvon (29 years)		Hamelin Pool (17 years)	
			Max.	Min.	Max.	Min.
January	30·8	22·6	37·2	21·0
February	32·0	23·1	37·1	21·8
March	30·1	21·9	35·0	20·1
April	28·1	18·7	30·0	16·9
May	25·9	14·9	25·5	13·4
June	23·1	13·0	21·8	11·4
July	21·9	11·0	20·9	9·5
August	22·4	11·3	22·3	9·5
September	23·8	13·8	25·5	11·2
October	25·6	16·4	29·0	13·6
November	27·0	18·7	32·2	16·0
December	28·9	20·8	34·9	18·8
Annual	26·7	17·2	29·3	15·3

many of their specimens were described as new species, the area contains a number of type localities. Some of their names also are commemorated in genera and species such as *Lechenaultia*, *Guichenotia*, *Eucalyptus baudiniana* *Angianthus cunninghamii*, *Angianthus milnei* and *Rhagodia gaudichaudiana*.



Figure 2.—Map of Dirk Hartog Island.

Mueller (1883) recorded 60 species based on early collections from Dirk Hartog Island, though many of the names he used are not in current use. They have been included under their current names in the flora list below excepting several species whose determination is doubtful and which are mentioned separately.

Although intermittent collecting continued on the mainland, after 1858 few plants were collected from the island until 1967 when a group of students from Wesley College, South Perth, visited it. In 1973, B. A. and A. G. Wells recorded 13 species, and in 1974 J. S. Beard made a small collection.

Our expedition of 1972 had the advantage of an excellent season, about 500 mm of rain having fallen between 1 January and 31 August 1972. Over 250 species were collected in flower or fruit. With flowering at its peak, many areas were extremely colourful, prominent species being *Acacia ligulata*, *Brachycome latisquamea*, *B. iberidifolia*, *Dampiera incana*, *Helipterum* spp., *Swainsona* spp. and *Thryptomene bacckeecea*. Some plants were not in flower, and collections at other seasons would probably



Figure 3.—Tall open-heath dominated by *Acacia ligulata*, 0.8 km W of homestead.

increase the list of indigenous flora to about 300 species. Several indeed have been added by recent visits of officers of the Wildlife Research Centre.

Vegetation

The vegetation has been mapped and described by Beard (1976), who recognised four communities on the island, designated by his own terminology. This paper describes five communities based on the terminology of Specht *et al.* (1974). They are correlated with Beard's classification as used in his text.

1. *Tall open-heath*.—(Figure 3). (Beard: shrub steppe, a₂₂ Si. x ZHc). This is by far the most extensive community, occupying the deep or shallow sand away from the coast and almost throughout the length of the island. It is usually dominated by *Acacia ligulata*, but several small areas are dominated by *Eucalyptus* of which there are 4 species. Other common tall shrubs are *Acacia coriacea*, *Pittosporum phylliracoides*, *Diplolaena grandiflora*, *Heterodendrum oleifolium* and *Alyogyne cuneiformis*. Lower shrubs, up to 1 m tall, include *Atriplex bunburyana*, *Thryptomene baeckeacea*, *Beaufortia dampieri*, *Pimela microcephala*, *Ptilotus obovatus* and *Cassia chatelainiana*. The spinifex *Plectrachne*

sp. is common, and the introduced Buffel Grass (*Cenchrus ciliaris*) has spread widely. The perennial scrambler *Brachycome latisquamea* is common.

In a few areas the vegetation is up to 3 m tall and should be termed tall shrubland, while in others it is sparse and becomes low shrubland or low open-shrubland.

2. *Low closed/open-heath with hummock grasses*.—(Figures 4, 5). (included with shrub steppe by Beard.) North of Sandy Point are areas of low heath, varying from open to closed, with an admixture of spinifex (*Plectrachne* sp. and *Triedia plurinervata*). The myrtles *Thryptomene baeckeacea* and *Melaleuca cardiophylla* are common, and *Acacia ligulata* is still frequent. South Western elements predominate in the other shrubs which include *Calytrix strigosa*, *Cryptandra nudiflora*, *Pityrodia atriplicina*, *Acacia? leptospermoides*, *Geleznowia verrucosa*, *Guichenotia ledifolia*, *Daviesia* aff. *collettioides* and *Keraudrenia hermanniifolia*. Two sedges were recorded—*Lepidobolus preissianus* and *Gahnia? lanigera*. Ephemeral herbs include *Brachycome iberidifolia*, *Swainsona* sp. and *Senecio lautus*, and the perennial *Brachycome latisquamea* is frequent. Occasionally the spinifexes are dominant almost as a hummock grassland.



Figure 4.—Low open-heath with hummock grassland, dominated by *Acacia ligulata* and *Triodia plurinervata*, N of Sandy Point Outcamp.

Formations similar to this or intermediate between it and the tall open-heath occur in other parts of the island, some apparently being the "full heath-spinifex community" described by Beard under mixed heath and spinifex.

Low very-open-heath.—(Figure 6). (Beard: mixed heath and spinifex, x ZHc. This term is not used by Specht but is used here for low heath (under 1 m tall) with cover less than 10%). The community occurs in shallow sand over limestone above rocky shores such as Quoin Bluff South and along the south-western coast. The shrubs include *Thryptomene baeckeacea*, *Leaevola crassifolia*, *Solanum orbiculatum*, *Frankenia pauciflora*, *Dampiera incana*, *Consonida gaudichaudii* and *Atriplex* sp. *Plectrachne* sp. is present, and ephemeral herbs include *Lotus cruentus*, *Brachycome iberidifolia* and *Calocephalus francisii*.

A variant of low very-open-heath occurs on sandy flats near the shore at Sandy Point and farther north (Beard: dwarf scrub XZi). The ubiquitous *Thryptomene baeckeacea* is the common shrub, with some *Myoporum* sp. Perennial herbs include *Carpobrotus rossii*, *Conostylis stydioides*, *Dicrastylis* sp. and *Spinifex longifolius*.

Hummock grassland.—(Beard: part of mixed heath and spinifex, x ZHc). Small areas tending towards hummock grassland among the low

heath have already been mentioned, but quite extensive areas occur over the hills of Herald Heights. *Triodia plurinervata* is usually dominant, with some *Plectrachne* sp. Shrubs are low and sparse, and include *Pimelea gilgiana*, *Olearia axillaris* and *Thryptomene baeckeacea*.

Low open-shrubland.—(Figure 7). (Beard: samphire community, K₃ Ci). A number of saline flats occur on the island such as those to the south and west of the homestead on which the old and the new airstrips lie. Samphires dominate them, especially species of *Arthrocnemum* and *Salicornia*. The halophytes *Limonium*, *Atriplex* and *Samolus* are common, and herbs occur such as *Senecio glossanthus*, *Angianthus microcephalus* and *Parietaria debilis*.

The only stand of mangroves on the island is a small population of *Avicennia marina* by a soak on a saline flat at Tetrodon Loop.

Heavily grazed areas around mills and small holding pens have been mostly stripped of indigenous vegetation. Introduced plants have taken over, though most are ephemeral and these areas would be almost bare except after rain. The species include *Lolium loliaceum*, *Hordeum leporinum*, *Koeleria phleoides*, *Melilotus indicus*, *Medicago polymorpha*, *Erodium cicutarium* and *Spergularia rubra*.



Figure 5.—Low open-heath, dominated by *Thryptomene baeckeacea* and *Plectrachne* sp., 5 km N of Cape Ransonnet.

There are extensive blown out sandy areas quite without vegetation, for example near Tetrodon Loop and Mystery Beach. Along the west coast, rocky shores even atop cliffs are kept bare of vegetation by salt spray, sometimes up to 100 m from the sea.

Flora

The known indigenous flora of Dirk Hartog Island is listed in Table 2 and the naturalised flora in Table 3. Both lists are alphabetical. Table 2 cites the species, family, habit and habitat. The distribution on the mainland in the South West (SW) and Erasmiean (E) Botanical Provinces is shown in the first two columns, while the third (SB) denotes species restricted to the Shark Bay area. Species are included in the South West Province if their only other occurrence outside it (other than Dirk Hartog Island) is Bernier and Dorre Islands.

Representation of the larger families of the indigenous flora is shown in the following list.

Asteraceae	37	Mimosaceae	8
Chenopodiaceae	20	Myoporaceae	7
Poaceae	18	Amaranthaceae	6
Myrtaceae	13	Brassicaceae	6
Papilionaceae	13	Euphorbiaceae	6
Goodeniaceae	9	Sterculiaceae	6
Liliaceae	9	Zygophyllaceae	6
Malvaceae	8	Solanaceae	5

There are 2 families with 4 species, 8 with 3 species, 9 with 2 species and 32 with 1 species. The total number of indigenous families is 67.

The largest genera are *Acacia* (8 species), *Angianthus* (7 species), *Arthrocnemum* and *Ptilotus* (both with 6 species), *Rhagodia* (5 species), *Eucalyptus*, *Helipterum*, *Melaleuca*, *Scaevola*, *Swainsona* and *Zygophyllum* (all with 4 species). The number of genera is 167.

Several species recorded by Mueller should be checked before they can be definitely listed for the island.

They are:

Acacia *spathulata* F. Muell.—probably *A. leptospermoides* Benth.

Casuarina *humilis* Otto et Dietr.—probably *C. helmsii* Ewart & Gordon.

Convolvulus *sepium* L.—? incorrect locality.

Dicrastylis *fulva* Drumm. et Harv.—probably undescribed.

Frankenia *laevis* L.—probably *F. pauciflora* DC.

Ptilotus *striatus* F. Muell.—probably *P. divaricatus* (Gaud.) F. Muell.



Figure 6.—Limestone cliff at Quoin Bluff South with low very open-heath.

Verticordia pennigera Endl.—? incorrect locality.

Melaleuca holosericea Schau.—? incorrect locality.

Excluding these, the known indigenous flora totals 259 species.

The flora of the island is of great interest phytogeographically. Morphologically the island populations, excluding of course several species known only on it, lie within the range of variation shown by those on the mainland. It is the size of the flora and more especially the geographical range of its components which demand attention. With 259 known indigenous species and an estimated total of about 300, the flora is easily the largest of any island off the lower western and southern Western Australian coasts. While this is expected on the much larger island that Dirk Hartog is, it is apparently also a much richer flora than that of the nearby peninsulas—Edel Land and Peron Peninsula. This is probably directly due to the higher rainfall on the island.

The flora is quite evenly divided between South Western and Eremean species, among which the following groups deserve mention.

1. Those apparently endemic to the island: *Gnephosis tenuissima*, *Stipa crinita*, *Trachymene elachocarpa*, *Olearia* sp. inedit., *Arthrocnemum* sp. inedit., *Chrysopogon* sp. inedit., *Scirpus* sp.
2. Those restricted to the Shark Bay area, i.e. the adjacent mainland, some extending along the coast north of Carnarvon. They are shown in the last column of Table 2 and total 18.
3. Those South Western species (54 in all) at their northern limit on the island, marked by an asterisk in Table 2. Some of these also represent the northern limit of the respective families in the South West Botanical Province. They are Casuarinaceae, Centrolepidaceae, Haemodoraceae, Orchidaceae and Restionaceae.
4. Those which are well isolated from their nearest known population on the mainland. These are *Helipterum oppositifolium* (nearest population Bullfinch); *Casuarina helmsii* (Arrino); *Melaleuca lanceolata* (Geraldton); *Neosciadium glochidiatum* (Drummond collection: ? near Perth); *Limosella australis* (Harvey).



Figure 7.—Low open-shrubland dominated by *Arthrocnemum* spp. on (new) airstrip flat.

The indigenous flora of Dirk Hartog Island is over twice that of Bernier and Dorre Islands (Royce in Ride *et al.* 1962), which lie just to the north and, though much smaller, are geologically similar but receive a lower rainfall. Recent collecting by K. F. Kenneally during post-fire regeneration studies on Dorre Island has added 16 species to that island's flora (Kenneally pers. comm.). The total for Dorre of 109 species and for Bernier of 96 species compares with 259 for Dirk Hartog. Discounting the marine *Halophila ovalis*, twenty-six species on Bernier and Dorre have not so far been collected on Dirk Hartog. Almost all are Ereman species, reflecting the lower rainfall on those islands. Of over 150 species on Dirk Hartog not recorded for Bernier and Dorre, the most interesting is the unnamed *Plectrachne*, common on Dirk Hartog but known otherwise only from Edel Land.

At the time of our visit the vegetation was generally in good condition, especially in the northern half of the island where there were no sheep. There was no sign of recent fire, and we understand that for many years fire has not been used in pastoral management on the island. There are few fire-adapted species on the island. Provided that populations of grazing and browsing animals do not build up enough to cause overgrazing, the flora should maintain itself without requiring a great deal of management.

Dirk Hartog Island: South West or Ereman Province?

Beard (1976) determined a precise boundary for the South West Botanical Province in this region (his Fig. 2 p. 13 and Fig. 3 p. 27), leaving most of Edel Land, Peron Peninsula and the islands in the Ereman Province. He concluded that the Dirk Hartog communities "should be placed within the Ereman Province while recognising their intermediate character." In reaching this conclusion he gave "due weight" to "floristics, physiognomy and habitat". However, his visit to the island was made in a dry season and he stated that the "whole impression is one of desolation and aridity". This contrasts with the excellent condition and flowering of the flora during our visit. Since a good proportion (62%) of the species are shrubs or perennial herbs there is always a cover, albeit often open, of vegetation.

Floristically the island is almost equally divided between the provinces but with a leaning to the South West. Of the named species in Table 2, 77 are South Western, 61 are Ereman and 102 are common to both. However a number of species listed as Ereman have taxonomic affinities with the South Western flora, e.g. *Beaufortia dampieri*, *Pileanthus limacis*, *Beyeria cyanescens*, *Dampiera incana*, *Lechenaultia sub-*

Table 2

The known indigenous flora of Dirk Hartog Island, arranged alphabetically with the distribution on the mainland shown in the three columns: SW—South West Botanical Province; E—Erebean Province; SB—Shark Bay area only. Species at their northern limit on Dirk Hartog Island are marked by an asterisk in the SW or E column.

	SW	E	SB		SW	E	SB
<i>Abutilon geranioides</i> (DC.) Benth. Malvaceae Scrambling shrub 1·3 m, fls pale yellow. In sand over limestone, among low open-heath.		X	X	<i>Angianthus strictus</i> (Steetz) Benth. Asteraceae .. Ephemeral herb; fls yellow. In loam, in open grazed area near mill.	X	X	
<i>Abutilon oxycarpum</i> F. Muell. Malvaceae .. Slender shrub to 50 cm; fls yellow inside with brown centres, brownish outside. In sand, in tall open-heath.		X		<i>Angianthus tomentosus</i> Wendl. Asteraceae .. Ephemeral herb.	X	X	
<i>Acacia bivenosa</i> DC. Mimosaceae		X		<i>Angianthus</i> sp. ASG 11362. Asteraceae .. Ephemeral herb; fls immature. In loam over limestone, in open grazed area.			
<i>Acacia coriacea</i> DC. Mimosaceae Spreading shrub to 2·5 m. On rocky, limestone flat near west coast, in low open-shrubland, and in sand in open-heath.		X		<i>Angianthus</i> sp. ASG 11471. Asteraceae .. Ephemeral herb aromatic; fls yellow. In limestone, in low very open-heath.			
<i>Acacia idiomorpha</i> A.Cunn. ex Benth. Mimosaceae X* Low, straggling shrub 30 cm. In sand, in low open-heath.	X*			<i>Anguillaria monantha</i> Endl. Liliaceae .. Bulbous herb, in fruit. In sand, in tall open-heath.	X*		
<i>Acacia* leptospermioides</i> Benth. Mimosaceae Sprawling shrub 40 cm. In sand, in tall open-heath.	X*			<i>Anthroche walcottii</i> F. Muell. Solanaceae .. Collected by Milne.	X*		
<i>Acacia leptospermioides</i> Benth. Mimosaceae X* Shrub to 3 m; bark smooth, grey. In sand, in tall open-heath.	X*			<i>Aphanopetalum clematideum</i> (Drumm. et Harv.) C. A. Gardn. Cunoniaceae .. Climber, fls cream-green. In sand, in low open-heath.	X*		
<i>Acacia ligulata</i> A.Cunn. ex Benth. Mimosaceae Spreading shrub to 2·5 m; bark smooth, grey, becoming fissured when old. Common throughout island, especially in sand, in tall open-heath and low open-heath.	X	X		<i>Aristida contorta</i> F. Muell. Poaceae .. Collected by Gaudichaud.		X	X
<i>Acacia tetragonophylla</i> F. Muell. Mimosaceae Spreading shrub to 1·7 m. In sand, in tall open-heath.	X	X		<i>Arthrocnemum bidens</i> Nees. Chenopodiaceae Sprawling, succulent shrub, ± dull green. On saline flat, in low open-shrubland.	X	X	
<i>Acacia</i> sp. Mimosaceae Shrub 1·5 m, in leaf only. In sand, in tall open-heath. Only 1 population seen.		X	X	<i>Arthrocnemum halocnemoides</i> Moq. Chenopodiaceae Shrub to 70 cm, ± yellow-green. On saline flat, in low open-shrubland.	X	X	
<i>Acanthocarpus preissii</i> Lehm. Liliaceae Straggling perennial herb. In sand, in tall open-heath.	X			<i>Arthrocnemum prinosum</i> Paulsen. Chenopodiaceae Succulent shrub. On saline flat, in low open-shrubland.		X	
<i>Acanthocarpus</i> sp. Liliaceae Tough perennial herb to 60 cm, forming clumps. In sand, in tall open-heath. A larger, more robust plant than <i>A. preissii</i> . Also occurs on the coastal plain west of the Cape Range.		X	X	<i>Arthrocnemum</i> sp. ASG 11609. Chenopodiaceae Sprawling, succulent perennial herb to 10 cm tall. On saline flat, in low open-shrubland.		X	
<i>Algyone cuneiformis</i> (DC.) Lewton. Malvaceae Shrub to 3 m; fl white with red centre (only 1 fl seen). In sand, in tall open-heath.	X	X	X	<i>Arthrocnemum</i> sp. ASG 11430. Chenopodiaceae Succulent shrub, red and green. On saline flat, in low open-shrubland.		X	
<i>Algyone pinonius</i> (Gaud.) Fryxell. Malvaceae X Shrub 1·3 m; fl mauve (only 1 fl seen). In sand, in tall open-heath.	X	X		<i>Arthrocnemum</i> sp. ASG 11454a. Chenopodiaceae Succulent shrub, ± bright green. On saline flat, in low open-shrubland.		X	X
<i>Amphibolis antarctica</i> (Labill.) Sond. et Aschers Potamogetonaceae Collected by Gaudichaud.				<i>Atriplex bimbryana</i> F. Muell. Chenopodiaceae Shrub to 1 m. In sand, on coastal dune by beach and in tall open-heath.	X	X	
<i>Amyema linophyllum</i> (Fenzl) Tiegh. Loranaceae X Collected by Milne.	X			<i>Atriplex vesicaria</i> Benth. Chenopodiaceae		X	
<i>Amyema preissii</i> (Miq.) Tiegh. Loranaceae Mistletoe on <i>Acacia ligulata</i> . In tall open-heath.	X	X		<i>Avicennia marina</i> (Forsk.) Vierh. Avicenniaceae Mangrove: shrub 3 m with pneumatophores. In saline mud by soak near coast. Only 1 small population seen.	X	X	
<i>Angianthus cunninghamii</i> (DC.) Benth. Asteraceae X	X	X		<i>Baeckea pentagonantha</i> F. Muell. Myrtaceae X* Collected by Milne.	X*		
<i>Angianthus microcephalus</i> (F. Muell.) Benth. Asteraceae X* Ephemeral herb. On saline flat, in low open-shrubland.	X*	X		<i>Bassia uniflora</i> (R.Br.) F. Muell. Chenopodiaceae Sprawling shrub 30 cm tall. In sand over limestone near coast, in tall open-heath.	X	X	
<i>Angianthus mihelii</i> Benth. Asteraceae Collected by Milne.		X		<i>Beaufortia dampieri</i> A. Cunn. ex Hook. Myrtaceae X Spreading shrub to 1·5 m tall; fls pale pink to white. On sand dunes, in tall open-heath.	X		

Table 2—continued

	SW	E	SB		SW	E	SB
<i>Beyeria cyanescens</i> (Muell. Arg.) Benth. Euphorbiaceae Much-branched shrub 35 cm, dioecious. In sand, in tall open-heath.	X	X		<i>Cassytha pabescens</i> R.Br. Lauraceae Parasitic climber. In tall open-heath.		X	X
<i>Bidens bipinnata</i> L. Asteraceae Ephemeral herb; fls yellow. On rocky, limestone flat near west coast, in low open-shrubland.		X		<i>Casuarina helmsii</i> Ewart and Gordon. Casuarinaceae Sprawling shrub 40 cm tall x 2 m broad. Rare, in sand in low closed/open-heath. In East Sandy Paddock, only male seen; in Blowhole Paddock, male and female seen.	X	X	
<i>Boerhavia chinensis</i> (L.) Aschers and Schweinf. Nyctaginaceae Sprawling perennial herb; fls deep pink. On rocky, limestone flat near west coast, in low open-shrubland.		X		<i>Centrolepis humillima</i> F.Muell. ex Benth. Centrolepidaceae On saline flat in low open-shrubland.	X*		
<i>Bossiaea rufa</i> R.Br. var. <i>foliosa</i> Benth. Papilionaceae Spreading shrub 30 cm; fls yellow and red. In sand, in tall open-heath.	X*			<i>Cephalopterum drummondii</i> A. Gray. Asteraceae Ephemeral herb; bracts yellow or white. In loam over limestone, in open grazed area.	X	X	
<i>Brachycome ciliaris</i> (Labill.) Less. Asteraceae Ephemeral herb; rays pale mauve. In sand over limestone, in low open-shrubland.	X	X		<i>Chamaesyce myrtoides</i> (Boiss.) Hassall. Euphorbiaceae Ephemeral herb.		X	
<i>Brachycome iberidifolia</i> Benth. Asteraceae Ephemeral herb; rays mauve. Common in many areas, in sand or on limestone. In open-heath, low-shrubland.	X	X		<i>Chorizema ericifolium</i> Meisn. Papilionaceae Shrub to 40 cm; fls yellow and red. In sand, in low open-heath/hummock grassland.	X	X	
<i>Brachycome latisquea</i> F.Muell. Asteraceae Scrambling shrub to 1.5 m; rays mauve, rarely white. In sand, in tall open-heath and low shrubland; fairly common.		X	X	<i>Chrysopogon</i> sp. ASG 11544. Poaceae Perennial grass with underground rhizomes. In sand near seashore.			
<i>Brachysema macrocarpum</i> Benth. Papilionaceae Perennial herb. In sand, in tall open-heath.		X	X	<i>Clematis microphylla</i> DC. Ranunculaceae Climber; fls white. In sand, in tall open-heath.	X		
<i>Cakile maritima</i> L. Brassicaceae Perennial herb; fls pink. In sand above beach by homestead.	X	X		<i>Commersonia gaudichaudii</i> J. Gay. Sterculiaceae Spreading shrub; fls white. In sand, in low very open-heath.	X*	X	
<i>Calandrinia polyandra</i> Benth. Portulacaceae Ephemeral herb with succulent lvs; fls bright pink inside, centres often darker, pale yellow outside. In sand, in open-shrub, and in limestone near sea.	X	X		<i>Conostylis stylioides</i> F.Muell. Haemodoraceae Caespitose perennial herb; fls yellow. In sand, in tall open-heath and in low very open-heath.	X*		
<i>Calandrinia</i> sp. Portulacaceae Succulent ephemeral herb, reddish. In sand over limestone, in low open-shrubland.				<i>Corynotheca micrantha</i> (Lindl.) Macbride. Liliaceae Sprawling perennial herb; fls pale pink to white. On coastal dune, in tall open-heath.	X		
<i>Calocephalus francisii</i> (F.Muell.) Benth. Asteraceae Ephemeral herb; fls white or pale yellow. In sand, in low open-heath.	X	X		<i>Cotula cotuloides</i> (Steetz) Druce. Asteraceae Ephemeral herb. In sand, in open grazed area by mill.	X	X	
<i>Calogyne herardiana</i> (Gaud.) F.Muell. Goodeniaceae Ephemeral herb; fls yellow. On sand dune, in low open-heath.	X	X		<i>Crassula colorata</i> (Nees) Ostenf. Crassulaceae Ephemeral herb. In sand, in tall open-heath.	X	X	
<i>Calotis multicaulis</i> (Turcz.) Druce. Asteraceae Ephemeral herb; rays white. In loam over limestone, in open grazed area.		X		<i>Cryptandra nudiflora</i> F.Muell. Rhamnaceae Low shrub. In sand, in low open-heath.	X*		
<i>Calytrix strigosa</i> A. Cunn. Myrtaceae Sprawling shrub 25 cm; fls purple, stamens yellow. In sand, in low open-heath.	X*			<i>Cymbopogon ambiguus</i> A. Camus. Poaceae Perennial grass. On sand dune, in low open-heath.	X	X	
<i>Capparis spinosa</i> L. var. <i>nummularia</i> (DC.) F. M. Bailey. Capparidaceae Shrub ± 1 m. In limestone, in tall open-heath.	X	X		<i>Cyperus bulbosus</i> Vahl. Cyperaceae Rhizomatous sedge; fls brown.		X	
<i>Carpobrotus rossii</i> (Haw.) Schwantes. Aizoaceae Prostrate perennial herb with succulent lvs; fls pale pink to white. In white sand, in low open-heath.	X	X		<i>Dampiera incana</i> R.Br. Goodeniaceae Perennial herb to 50 cm; fls deep blue. In sand, in tall and low open-heath.		X	X
<i>Cassia chatelainiana</i> Gaud. Caesalpinaceae Shrub to 1 m; fls bright yellow. In sand, in tall open-heath.	X	X		<i>Danthonia racemosa</i> R.Br. Poaceae Collected by Gaudichaud.	X*		
<i>Cassytha nodiflora</i> Meisn. Lauraceae Parasitic climber. In low open-shrubland near cosat.	X			<i>Daucus glochidiatus</i> (Labill.) Fisch. Mey. and Avenell. Apiaceae Ephemeral herb. In sand, in tall open-heath.	X	X	
				<i>Daviesia</i> aff. <i>collettioides</i> Meisn. Papilionaceae Much-branched shrub 40 cm; fls yellow and red. In sand, in tall open-heath.	X		
				<i>Dianella revoluta</i> R.Br. Liliaceae Caespitose perennial herb; fls blue. In sand, in tall open-heath.	X	X	

Table 2—continued

	SW	E	SB		SW	E	SB
<i>Dichopogon strictus</i> (R.Br.) Baker. Liliaceae Herb with tubers; fls mauve. In sand, in tall open-heath.	X*			<i>Eucalyptus foecunda</i> Schau. Myrtaceae Dense, sprawling mallee 1-2 m tall; lower bark rough, upper smooth, fls white. In sand, in tall open-heath.	X		
<i>Dicrastylis</i> sp. Chloanthaceae Perennial herb, in leaf only. In sand above beach by homestead, and at Sandy Point in low shrubland.		X	X	<i>Eucalyptus tamala</i> Carr & Carr. Myrtaceae Sprawling mallee 1.5 m tall; bark rough at base, smooth above. In sand, in tall open-heath.	X		
<i>Diplolaena grandiflora</i> Desf. Rutaceae Shrub to 2 m; bracts red, fls orange to pale green. Common, especially in sand in tall open-heath.	X	X		<i>Eulalia fulva</i> (R.Br.) O. Kuntze. Poaceae Perennial grass; fls brown. In limestone, in low very open-heath.		X	
<i>Diplolaena microcephala</i> Desf. Rutaceae Shrub to 1.7 m; fls red-pink. In sand, in tall open-heath.	X*			<i>Euphorbia cremophila</i> A. Cunn. ex Hook. Euphorbiaceae Ephemeral herb with latex. In sand, in low open-heath/hummock grassland	X	X	
<i>Dodonaea aptera</i> Miq. Sapindaceae Shrub 70 cm. In sand, in tall open-heath.	X*			<i>Euphorbia sharkoensis</i> Baill. Euphorbiaceae Ephemeral herb.	X		
<i>Dodonaea inaequalifolia</i> Turcz. Sapindaceae Shrub to 1.3 m; fr red and green, \pm viscid. In sand over limestone cliff top, in tall open-heath.	X*	X		<i>Exocarpos aphyllus</i> R.Br. Santalaceae Much-branched shrub 2 m; fls greenish-yellow. In sand, in tall open-heath.	X	X	
<i>Dysphania plantaginella</i> F.Muell. Chenopodiaceae Ephemeral herb; fls pale green. In sand over limestone, in low open-heath.		X		<i>Frankenia cinerea</i> DC. Frankeniaceae Small shrub to 10 cm tall; fls white. On saline flat, in low open-shrubland.		X	
<i>Enchylaena tomentosa</i> R.Br. Chenopodiaceae Shrub 70 cm; fr orange. In sand, in tall open-heath.	X	X		<i>Frankenia pauciflora</i> DC. Frankeniaceae	X	X	
<i>Eriopogon caeruleus</i> (Gaud.) N. T. Burbidge. Poaceae Small, caespitose, perennial grass; fls lead-green. In sand over limestone on cliff top, in low open-heath.		X		<i>Galnia? lanigera</i> (R.Br.) Benth. Cyperaceae Caespitose perennial sedge. In sand over limestone, in low open-heath.	X*		
<i>Eragrostis? brownii</i> (Kunth) Nees. Poaceae Small ephemeral grass. In sand, in tall open-heath.	X			<i>Geleznowia verrucosa</i> Turcz. Rutaceae Small shrub to 35 cm; fls yellow. In sand, in low closed-heath	X*		
<i>Eragrostis dielsii</i> Pilger. Poaceae Prostrate ephemeral grass; fls green-purplish. In loam over limestone, in open grazed area by mill.	X	X		<i>Glycine tabacina</i> (Labill.) Benth. Papilionaceae Slender climber; fls deep pink In sand over limestone, in low open-heath	X	X	
<i>Eremophila clarkii</i> F.Muell. Myoporaceae Spreading shrub 1 m tall; fls pale to deep pink. In sand, in tall open-heath.	X	X		<i>Gnaphalium luteoalbum</i> L. Asteraceae Ephemeral herb. In sand by homestead.	X	X	
<i>Eremophila glabra</i> (R.Br.) Ostenf. Myoporaceae Shrub 25-130 cm; fls red (3 variants collected). In sand, in tall and low open-heath.	X	X		<i>Gnaphalodes condensatum</i> A. Gray. Asteraceae Ephemeral herb; fls cream-green. In sand over limestone, in low open-heath.	X	X	
<i>Eremophila oldfieldii</i> F.Muell. Myoporaceae Shrub to 1.5 m; fls dull red. In sand over limestone on cliff top, in tall open-heath.	X	X		<i>Gnephosis macrocephala</i> Turcz. Asteraceae Ephemeral herb; fls yellow. In sand, in open-heath.	X		
<i>Eriachne mucronata</i> R.Br. Poaceae Caespitose perennial grass. In sand, in tall open-heath.		X		<i>Gnephosis skirrophora</i> (Sond.) Benth. Asteraceae Collected by Milne.	X	X	
<i>Eriochilus dilatatus</i> Lindl. Orchidaceae Orchid with tuber; in old fruit. On sandy hill, in low open-heath.	X*			<i>Gnephosis? tenuissima</i> Cass. Asteraceae	X		
<i>Erodium angustilobum</i> Carolin. Geraniaceae Ephemeral herb.		X		<i>Goodenia</i> sp. ASG 11508. Goodeniaceae Herb with underground stolons; fls yellow. In sand, in low open-heath.			
<i>Erodium cygnorum</i> Nees subsp. <i>cygnorum</i> . Geraniaceae Ephemeral herb.	X	X		<i>Grevillea stenophylla</i> W. V. Fitzg. Proteaceae Sprawling shrub 40 cm; fls cream on reddish pedicels. In sand, in closed-heath.	X*		
<i>Eucalyptus baudiniana</i> Carr & Carr. Myrtaceae Sprawling mallee 1.5 m. In sand, in tall open-heath.	X			<i>Guichenotia ledifolia</i> J. Gay. Sterculiaceae Spreading shrub to 80 cm; fls pale pink. In sand, in tall open-heath.	X*		
<i>Eucalyptus dongarraensis</i> Maiden & Blakely. Myrtaceae Mallee 1-2.5 m; bark rough at base, exfoliating in broad, \pm smooth strips above. In sand or sand over limestone in tall open-heath.	X	X		<i>Gyrostemon ramulosus</i> Desf. Gyrostemonaceae Tree 3 m. male; no female seen. In sand, as emergent in tall open-heath.	X	X	
				<i>Halcania littoralis</i> Gaud. Boraginaceae Shrub 40 cm; fls deep blue. In sand, in low open-heath/hummock grassland.	X		
				<i>Haloragis gossei</i> F. Muell. Haloragaceae Ephemeral herb.		X	

Table 2---continued

	SW	E	SB		SW	E	SH
<i>Haloragis trigonocarpa</i> F. Muell. Haloragaceae Ephemeral herb. In loam over limestone, in open grazed area.		X		<i>Leptomeria spinosa</i> (Lehm.) DC. Santalaceae Collected by Cunningham.	X		
<i>Hannafordia quadrivalvis</i> F. Muell. Sterculiaceae Shrub 35 cm; fls pale yellow, brown outside. In sand, in tall open-heath.	X	X		<i>Limonium salicorniaceum</i> (F. Muell.) Kuntze. Plum- baginaceae Perennial herb; fls white. On saline flat, forming closed herbland with <i>Samolus. Atriplex</i> , etc. around small soak.		X	
<i>Helipterum condensatum</i> F. Muell. Asteraceae Ephemeral herb; bracts white; fls yellow. On coastal dune, in tall open-heath.	X	X		<i>Limosella australis</i> R. Br. Scrophulariaceae Ephemeral herb; fls white In loam over limestone, in open grazed area by mill.	X*		
<i>Helipterum humboldtianum</i> (Gaud.) DC. Asteraceae Ephemeral herb; fls bright yellow. In sand, in tall open-heath.	X	X		<i>Loania</i> sp. Loganiaceae	X		
<i>Helipterum oppositifolium</i> S. Moore. Asteraceae Ephemeral herb; bracts cream-white and bronze. In sand over limestone, in low open-heath.		X*		<i>Lotus cruentus</i> Court. Papilionaceae Ephemeral herb; fls maroon. In sand, in low open-heath near coast.		X	
<i>Helipterum polycephalum</i> (A. Gray) Benth. Aster- aceae Ephemeral herb; fls cream. In sand over limestone, in shelter of shrubs in tall open-heath.	X			<i>Loxocarya flexuosa</i> (R. Br.) Benth. Restionaceae Caespitose perennial sedge. In sand, in low open-heath.	X*		
<i>Heterodendrum oleifolium</i> Desf. Sapindaceae Shrub to 3 m. In limestone, in tall open-heath.		X		<i>Lysiana murrayi</i> (F. Muell. et Tate) Tiegh. Lorantha- ceae Mistletoe on <i>Acacia lignata</i> .		X	
<i>Hymenolobus procumbens</i> (L.) Nuttall. Brassicaceae Ephemeral herb. In soil pockets on limestone by sea, and on saline flat near airstrip.	X*			<i>Melaleuca cardiophylla</i> F. Muell. Myrtaceae Shrub. In sand, in tall and low open-heath.	X	X	
<i>Indigofera boviparda</i> A. Morrison. Papilionaceae Sprawling perennial herb; fls deep pink. In sand, in low open-heath.		X		<i>Melaleuca</i> aff. <i>heugelij</i> Endl. Myrtaceae Sprawling shrub 1 m tall x 4 m broad; fls pink. In sand or limestone, in low open-heath.	X*		
<i>Jasminum calcareum</i> F. Muell. Oleaceae Small shrub or straggling climber; fls white, sweetly scented. In sand, in tall open-heath.		X		<i>Melaleuca lanceolata</i> Otto. Myrtaceae Spreading shrub or tree to 4 m; bark grey, stringy. In shell grit near saline flat.	X*		
<i>Juncus bufonius</i> L. Juncaceae In sand, in open grazed area by mill.	X			<i>Melaleuca?</i> <i>oldfieldii</i> F. Muell. Myrtaceae	X*		
<i>Kennedia prostrata</i> R. Br. Papilionaceae Collected by Gaudichaud	X*			<i>Millotia myosotidifolia</i> (Benth.) Steetz. Asteraceae Ephemeral herb; fls white. On sand dunes in open-heath near coast.	X	X	
<i>Keraudrenia hermannifolia</i> J. Gay. Sterculiaceae Shrub to 35 cm; fls purple with yellow stamens. In sand, in tall open-heath.	X			<i>Mirbelia ramulosa</i> (Benth.) C. A. Gardn. Papilion- aceae Sprawling shrub, fls yellow and red. In sand, in low open-heath/hummock grassland.	X	X	
<i>Lasiopetalum angustifolium</i> W. V. Fitzg. Sterculiaceae Spreading shrub to 40 cm tall; fls pale pink. In sand in tall open-heath.	X			<i>Myoporum acuminatum</i> R. Br. Myoporaceae Shrub 1 m; fls white. On coastal dune, in tall open-heath.	X	X	
<i>Lawrenzia densiflora</i> (Bak.f.) Melville. Malvaceae In sand, in tall open-heath.		X		<i>Myoporum adscendens</i> R. Br. Myoporaceae	X		
<i>Lawrenzia</i> sp. Malvaceae				<i>Myoporum deserti</i> A. Cunn. ex Benth. Myoporaceae Shrub 50 cm. In sand, in open-heath.	X	X	
<i>Lechenaultia linarioides</i> DC. Goodeniaceae Tangled perennial herb 1 m; fls yellow and red. In sand, in low open-heath.	X*			<i>Myoporum tetrandrum</i> (Labill.) Domin. Myoporaceae Collected by Cunningham and Milne.	X*		
<i>Lechenaultia subcymosa</i> Gardn. & George. Goodeni- aceae Perennial herb; fls pale mauve. In sand over limestone, in low open-heath.		X	X	<i>Neosciadum glochidiatum</i> (Benth.) Domin. Apiaceae Ephemeral herb; fls cream. On saline flat, in low open-shrubland.	X*		
<i>Lepidium linifolium</i> (Desv.) Benth. Brassicaceae Straggling ephemeral herb to 1 m tall, fls white. In sand, in tall open-heath.	X	X		<i>Nicotiana occidentalis</i> Wheeler. Solanaceae Ephemeral herb; fls pale cream. In sand, in tall open-heath.	X	X	
<i>Lepidium pseudo-ruderale</i> Thell. Brassicaceae Slender ephemeral herb. In sand, in mustering yard.	X*			<i>Nitraria schoberi</i> L. Zygophyllaceae Much-branched shrub to 2 m; fls pale greenish- cream. On sand dune by coast, in tall open-heath.	X	X	
<i>Lepidium rotundum</i> DC. Brassicaceae Ephemeral herb. In sand, in tall open-heath.	X	X		<i>Olearia axillaris</i> (DC.) Benth. var. <i>obovata</i> Benth. Asteraceae	X		
<i>Lepidobolus preissianus</i> Nees. Restionaceae Caespitose sedge, dioecious. In sand, in low open-heath.	X*			<i>Olearia pineloides</i> (DC.) Benth. Asteraceae		X*	
				<i>Olearia</i> sp. ASG 11568. Asteraceae Straggling shrub, rays white. In limestone, in tall open-heath.			

Table 2—continued

	SW	E	SB		SW	E	SB
<i>Opercularia spermacoea</i> Labill. Rubiaceae Perennial herb to 35 cm. In sand, in low open-heath.	X*			<i>Porana sericea</i> (Gaud.) F. Muell. Convolvulaceae Climber; fls blue-purple. In sand, in tall open-heath.	X	X	
<i>Ophioglossum lusitanicum</i> L. subsp. <i>coriaceum</i> (A. Cunn.) Clausen. Ophioglossaceae In sandy pockets on limestone, in low open-heath.	X	X		<i>Poranthera microphylla</i> Brongn. Euphorbiaceae Ephemeral herb. In sand, in tall open-heath.	X	X	
<i>Oxalis corniculata</i> L. Oxalidaceae Fls yellow. In shelter of shrubs of sandy depression, in tall open-heath.	X	X		<i>Ptilotus alexandri</i> Benl. Amaranthaceae Ephemeral herb. In sand, in tall open-heath.		X	X
<i>Paractaneum novae-hollandiae</i> Beauv. Poaceae Ephemeral grass; fls purplish. In sand, in mustering yard.		X		<i>Ptilotus divaricatus</i> (Gaud.) F. Muell. Amaranthaceae Straggling perennial herb; fls pink. In sand, in low open-heath.	X	X	
<i>Parietaria debilis</i> Forst. f. Urticaceae Ephemeral herb; stems red, fls green. On saline flat, in low open-shrubland, and in limestone by sea.	X	X		<i>Ptilotus exaltatus</i> (Nees) Benth. Amaranthaceae Ephemeral herb; fls pink. In sand, in tall open-heath.	X	X	
<i>Paspalidium gracile</i> (R.Br.) Hughes. Poaceae Perennial grass; fls green. On rocky limestone near coast, in low open-shrubland.	X	X		<i>Ptilotus gaudichaudii</i> (Steud.) J. M. Black var. <i>parviflorus</i> (Benth.) Benl. Amaranthaceae Ephemeral herb; fls yellow. In sand, in tall open-heath.	X	X	
<i>Pentstemon linearis</i> Dene. Asclepiadaceae Climber; fls pale brown-green. In sand, in tall open-heath.		X		<i>Ptilotus obovatus</i> (Gaud.) F. Muell. Amaranthaceae Shrub to 70 cm; fls pink.	X	X	
<i>Phyllanthus? crassifolius</i> Muell. Arg. Euphorbiaceae Small shrub. In limestone, in low shrubland.	X			<i>Ptilotus villosiflorus</i> F. Muell. Amaranthaceae Ephemeral herb; fls cream-green and pale pink. On sand dune by coast, in open-heath.	X	X	
<i>Pileanthus linacis</i> Labill. Myrtaceae Sprawling shrub to 70 cm tall x 3 m broad, fls pale pink. In limestone soil, on cliffs by sea.		X	X	<i>Rhagodia crassifolia</i> R.Br. var. <i>latifolia</i> Benth. Chenopodiaceae Collected by Gaudichaud.		X	X
<i>Pinelea gilgiana</i> E. Pritzel. Thymelaeaceae Shrub to 35 cm, dioecious; fls white, mostly over. In sand, in hummock grassland and low shrubland.	X*			<i>Rhagodia gaudichaudiana</i> Moq. Chenopodiaceae Shrub to 1.3 m; fruit succulent red.	X	X	
<i>Pinelea microcephala</i> R.Br. Thymelaeaceae Shrub to 1.5 m, dioecious; male fls cream; fr orange or red. In sand, in tall and low open-heath and low shrubland.	X	X		<i>Rhagodia prelysi</i> Moq. Chenopodiaceae Sprawling shrub. In sand, in tall open-heath.			
<i>Pittosporum phyllitoides</i> DC. Pittosporaceae Tree to 3 m; fls cream. In sand, as emergent in tall open-heath, and at base of cliff near sea.	X	X		<i>Rhagodia</i> sp. ASG 11503. Chenopodiaceae Shrub 40 cm. In sand over limestone, in low open-heath.			
<i>Pityrodia atriplicina</i> (F. Muell.) F. Muell. ex Benth. Chloanthaceae Shrub 1 m; fls pink. In sand, in low closed-heath/hummock grassland.	X*			<i>Rulingia cygnorum</i> (Steud.) C. A. Gardn. Sterculiaceae Shrub to 40 cm; fls cream. In sand over limestone, in low open-heath.	X*		
<i>Pityrodia cuneata</i> (Gaud.) Benth. Dieracystylidaceae Much-branched shrub to 1 m; fls pale pink, spotted. In sand, in low open-heath.	X			<i>Ruppia maritima</i> L. Ruppiceae Aquatic herb. In pool on saline flat.	X*	X	
<i>Plantago varia</i> R.Br. Plantaginaceae In loam over limestone, in open grazed area.	X	X		<i>Salicornia blackiana</i> Ulbrich. Chenopodiaceae Shrub, red and green. On saline flat, in low open-shrubland.	X		
<i>Plectrachne</i> sp. Poaceae Spinifex; fls straw-pale purple. Common, especially in sand, in tall or low open-heath and hummock grassland.	X*	X		<i>Salsola kali</i> L. subsp. <i>ruthenica</i> (Iljen) Soo. Chenopodiaceae On sand dunes by coast.	X	X	
<i>Podolepis canescens</i> A. Cunn. ex DC. Asteraceae Ephemeral herb; fls yellow.	X	X		<i>Samolus repens</i> (Forst.) Pers. Primulaceae In limestone, by coast.	X	X	
<i>Podolepis gardneri</i> G. L. Davis. Asteraceae		X		<i>Santalum spicatum</i> (R.Br.) D.C. Santalaceae Shrub. In sand, in tall open-heath.	X	X	
<i>Podotheca angustifolia</i> (Labill.) Less. Asteraceae Ephemeral herb; fls pale yellow. In sand, in tall open-heath.	X*			<i>Sarcostemma australe</i> R.Br. Asclepiadaceae Shrub to 1.5 m with latex; fls cream. In sand, in tall open-heath.	X	X	
<i>Podotheca gnaphalioides</i> Grah. Asteraceae Ephemeral herb. In sand, in tall open-heath.	X*	X		<i>Scaevola crassifolia</i> Labill. Goodeniaceae Shrub to 1 m; fls white or pale blue. In sand, in low open-heath.	X	X	
				<i>Scaevola holosericea</i> De Vr. Goodeniaceae Perennial herb to 40 cm; fls pale blue. In sand, in tall open-heath.	X	X	

Table 2—continued

	SW	E	SB		SW	E	SB
<i>Scaevola spinescens</i> R.Br. Goodeniaceae	X	X		<i>Tetragonia amplexicoma</i> (Miq.) Hook.f. Aizoaceae	X*		
Divaricately-branched shrub to 70 cm; fls white.				Straggling shrub, fls yellow.			
In sand, in tall open-heath.				In sand, in tall open-heath.			
<i>Scaevola tomentosa</i> Gaud. Goodeniaceae	X	X		<i>Tetragonia diptera</i> F. Muell. Aizoaceae ..		X	X
Much-branched shrub to 1.5 m; fls gold, turning				Ephemeral herb.			
orange, anthers brown.				In sand at base of low cliff.			
In sand, in tall open-heath.				<i>Threlkeldia diffusa</i> R.Br. Chenopodiaceae	X	X	
<i>Scirpus cernuus</i> Vahl. Cyperaceae	X*			Diffuse perennial herb, lvs succulent.			
In limestone, in open grazed area.				In sand by homestead.			
<i>Scirpus</i> sp. ASG 11610. Cyperaceae				<i>Thryptomene haeckeeana</i> F.Muell. Myrtaceae		X	
Small ephemeral sedge.				Sprawling shrub to 50 cm tall x 1 m broad; fls			
On saline flat, in low open-shrubland.				pink.			
<i>Senecio glossanthus</i> (Sond.) Belcher. Asteraceae	X	X		Common, in sand and limestone, in tall and low			
Ephemeral herb.				open-heath.			
On saline flat, in low open-shrubland.				<i>Thysanotus patersonii</i> R.Br. Liliaceae	X	X	
<i>Senecio laetus</i> Willd. Asteraceae	X	X		Twining herb with tubers, fls pale purple.			
Perennial herb; fls yellow.				In sand over limestone, in tall open-heath.			
In sand or limestone, in low open-heath.				<i>Thysanotus speckii</i> Brittan. Liliaceae		X	
<i>Sida calyxhymentia</i> J. Gay. Malvaceae	X	X		In shelter of shrubs, in sand in low very open-			
Shrub 70 cm; fls pale yellow.				heath.			
In sand, in tall open-heath.				<i>Trachymene elachocarpa</i> (F.Muell.) B. L. Burt.			
<i>Sida corrugata</i> Lindl. Malvaceae		X		Apiaceae	X		
<i>Solanum lasiophyllum</i> Dun. Solanaceae	X	X		Ephemeral herb; fls white.			
<i>Solanum</i> aff. <i>oldfieldii</i> F.Muell. Solanaceae				In sand, in low open-heath.			
Small shrub 5-40 cm, suckering; fls purple.				<i>Trachymene</i> aff. <i>pilosa</i> Sm. Apiaceae			
In sand, in tall open-heath.				Tiny ephemeral herb; fruit ± smooth.			
<i>Solanum orbiculatum</i> Dun. Solanaceae	X	X		In sand, in open-heath.			
Spreading shrub to 50 cm; fls pale purple.				<i>Tribulus occidentalis</i> R.Br. Zygophyllaceae		X	
On sand dune near coast.				Near homestead.			
<i>Spinifex longifolius</i> R.Br. Poaceae ..	X	X		<i>Trichodesma zeylanicum</i> (L.) R.Br. Boraginaceae		X	
Perennial grass, dioecious.				Collected by Milne.			
On coastal dunes.				<i>Tricoryne elatior</i> R.Br. Liliaceae	X		
<i>Sporobolus virginicus</i> (L.) Kunth. Poaceae	X	X		Collected by Gaudichaud.			
Perennial rhizomatous grass; fls purplish.				<i>Triglochin calcitrapa</i> Hook. var. <i>isingiana</i> Black.			
In sand, in low open-heath near coast.				Juncaginaceae	X	X	
<i>Spyridium complicatum</i> F.Muell. Rhamnaceae	X*			Ephemeral herb.			
Rounded shrub to 40 cm, with old fls.				In sand, in open grazed area by mill.			
In sand, in low open-heath.				<i>Triglochin mucronata</i> R.Br. Juncaginaceae	X*		
<i>Spyridium?</i> <i>divaricatum</i> Benth. Rhamnaceae	X			Ephemeral herb.			
Small, much-branched shrub.				In sand, in open grazed area by mill.			
In sand, in low open-heath.				<i>Triglochin trichophora</i> Nees. Juncaginaceae	X		
<i>Stackhousia viminea</i> Sm. Stackhousiaceae	X	X		Ephemeral herb.			
Ephemeral herb; fls yellow.				In sand, in tall open-heath.			
In sand, in tall open-heath.				<i>Triodia plurinervata</i> N.T. Burbidge. Poaceae		X	
<i>Stenopetalum sphaerocarpum</i> F.Muell. Brassicaceae	X*			Spinifex, in clumps to 40 cm tall x 2 m broad;			
Ephemeral herb; fls pale yellow.				foliage fine, bright green.			
In sand over limestone, in low open-heath.				In sand, in low open/closed-heath with hummock			
<i>Stipa crinita</i> Gaud. Poaceae	X*			grassland.			
In sand, in open-heath.				<i>Vittadinia</i> sp. Asteraceae	X	X	
<i>Stipa elegantissima</i> Labill. Poaceae	X	X		Ephemeral herb; rays pale mauve, fls yellow.			
Perennial grass.				In sand over limestone, in tall open-heath.			
<i>Stipa</i> sp. ASG 11394. Poaceae				<i>Wahlenbergia</i> sp. Campanulaceae			
On sand dune by coast, in open-heath and in low				Ephemeral herb; fls pale blue.			
open-shrubland.				In sand over limestone, in low open-heath.			
<i>Stylobasium spathulatum</i> Desf. Stylobasiaceae	X			<i>Waltzia citrina</i> (Benth.) Steetz. Asteraceae	X	X	
Shrub to 1 m.				Ephemeral herb; fls yellow.			
In sand, in open-heath.				In sand, in tall open-heath.			
<i>Swainsona beasleyana</i> F.Muell. subsp. <i>elegantoides</i>		X		<i>Waltzia podolepis</i> (Gaud.) Steetz. Asteraceae		X	X
A.Lee. Papilionaceae				Ephemeral herb.			
Ephemeral herb; fls maroon-pink, turning blue,				In sand, in open-heath.			
eye pale yellow.				<i>Westingia rigida</i> R.Br. Lamiaceae	X		
In sand over limestone, on sea cliffs.				Much-branched shrub to 70 cm; fls white.			
<i>Swainsona kingii</i> F.Muell. subsp. <i>kingii</i> . Papilionaceae		X		In sand, in tall open-heath.			
Prostrate ephemeral herb; fls maroon.				<i>Zygophyllum ammophilum</i> F.Muell. Zygophyllaceae		X	
In limestone, in tall open-heath.				Ephemeral herb.			
<i>Swainsona phacoides</i> F.Muell. subsp. <i>grandiflora</i>		X		In sand, in low open-heath.			
(Benth.) A.Lee. Papilionaceae				<i>Zygophyllum aurantiacum</i> Lindl. Zygophyllaceae	X	X	
Prostrate ephemeral herb, scapes erect; fls				Straggling perennial herb; fls pale yellow.			
maroon, turning blue, eye yellow.				In sand, in open-heath.			
In sand, in low open-heath.				<i>Zygophyllum</i> aff. <i>aurantiacum</i> Lindl. Zygophyllaceae			
<i>Swainsona</i> sp. ASG 11570. Papilionaceae				Much-branched perennial herb; fls white.			
Prostrate ephemeral herb; fls pink.				On sand dune by coast, in open-heath.			
In limestone, in tall open-heath.				<i>Zygophyllum</i> aff. <i>fruticulosum</i> DC. Zygophyllaceae			

Table 3

Exotic species naturalised on Dirk Hartog Island.

Species	Family	Place of Origin
<i>Anagallis arvensis</i> L. var. <i>caerulea</i> Gouan	Primulaceae	Europe
<i>Arctotheca calendula</i> (L.) Levyns	Asteraceae	South Africa
<i>Asphodelus fistulosus</i> L.	Liliaceae	Mediterranean region
<i>Avena barbata</i> Brot.	Poaceae	Mediterranean region
<i>Brassica tournefortii</i> Gouan	Brassicaceae	Mediterranean region
<i>Briza minor</i> L.	Poaceae	Mediterranean region
<i>Bromus diandrus</i> Roth	Poaceae	Mediterranean region
<i>Bromus hordeaceus</i> L.	Poaceae	Mediterranean region
<i>Cenchrus ciliaris</i> L.	Poaceae	Africa/N. India
<i>Cenchrus setigerus</i> Vahl	Poaceae	Africa/N. India
<i>Centaurea medionensis</i> L.	Asteraceae	Europe—W. Asia
<i>Cerastium glomeratum</i> Thuill.	Caryophyllaceae	Europe
<i>Chenopodium murale</i> L.	Chenopodiaceae	Europe
<i>Cynodon dactylon</i> (L.) Pers.	Poaceae	South Africa
<i>Diplaxis muralis</i> (L.) DC.	Brassicaceae	Europe
<i>Ehrharta brevifolia</i> Schrad.	Poaceae	South Africa
<i>Emex australis</i> Steinh.	Polygonaceae	South Africa
<i>Erodium cicutarium</i> (L.) L.Her. ex Ait.	Geraniaceae	Europe—S. Asia
<i>Hordeum leporinum</i> Link.	Poaceae	Mediterranean region
<i>Hypochaeris glabra</i> L.	Asteraceae	Europe—Asia
<i>Koeleria phleoides</i> (Vill.) Pers.	Poaceae	Mediterranean region
<i>Lavatera cretica</i> L.	Malvaceae	Mediterranean region
<i>Lotium loliaceum</i> (Bory et Chaub.) Hand-Mazz.	Poaceae	Mediterranean region
<i>Medicago polymorpha</i> L. subsp. <i>polymorpha</i>	Papilionaceae	Mediterranean region
<i>Medicago indicus</i> (L.) All.	Papilionaceae	Europe—W. Asia
<i>Nicotiana glauca</i> R. Graham	Solanaceae	Argentina
<i>Olea annua</i> L.	Poaceae	Europe—W. Asia
<i>Polycarpon tetraphyllum</i> (L.) L.	Caryophyllaceae	Europe
<i>Ricinus communis</i> L.	Euphorbiaceae	India—tropical Africa
<i>Silene gallica</i> L.	Caryophyllaceae	Europe
<i>Sisymbrium irio</i> L.	Brassicaceae	Mediterranean region
<i>Sisymbrium orientale</i> L.	Brassicaceae	Mediterranean region
<i>Solanum nodiflorum</i> Jacq.	Solanaceae	N. & S. America
<i>Sonchus oleraceus</i> L.	Asteraceae	Europe—Asia
<i>Spergularia rubra</i> (L.) J. & C. Presl.	Caryophyllaceae	Europe
<i>Trospernum picroides</i> (L.) Desf.	Asteraceae	Mediterranean region

pymosa and *Brachysema macrocarpum*. Of the three dominant species on the island—*Acacia ligulata*, *Thryptomene baeckeacea* and *Plectrachne* sp.—the *Acacia* and *Thryptomene* extended well into the South West Province while the *Plectrachne*, though of a typical Eremean genus, is restricted to the island and Edel Land and is marginally Eremean. Several major families which characterise the South West Province are lacking (e.g. Epacridaceae, Droseraceae, Dilleniaceae) or poorly represented (e.g. Proteaceae [1 sp.], Orchidaceae [1 sp.], Haemodioraceao [1 sp.]).

If life-form is considered, it can be seen that the woody shrubs are more South Western than Eremean, while the ephemeral herbs are predominantly Eremean. Of the 77 purely South West species on the island, 42 are shrubs or perennial herbs, while of the 61 Eremean only 24 are shrubs or perennial herbs.

Vegetation formation (physiognomy) presents a clearer picture. The widespread open-heath can be considered intermediate, though similar formations but lacking *Triodia* or *Plectrachne* occur near the coast between Tamala and Kalbarri to the south of Shark Bay.

It is clearly difficult to place Dirk Hartog Island in either Province, and it may be best left in a "Transitional zone". However if placed in one or the other the South West Province is preferable because

1. a majority of the species present are either South Western or have strong South Western affinities;
2. the vegetation formations, apart from hummock grassland, are more representative of the South West than the Eremean.

Naturalised flora

Table 3 lists 36 introduced species which are considered naturalised. The country of origin is given after the family. Most have their origin in Europe (especially the Mediterranean region) or South Africa. Several grasses have probably been introduced as pasture species, e.g. *Cenchrus ciliaris*, *C. setigerus* and *Bromus diandrus*. The others have probably come to the island with sheep. All are common weeds of south western Australia except the two *Cenchrus* species. There are 12 Poaceae, 5 Asteraceae, 4 Brassicaceae, 4 Caryophyllaceae, 2 Papilionaceae, 2 Solanaceae and 1 each of seven other families. Thirty are ephemeral herbs, 4 are perennial and 2 are shrubs.

Fauna

Mammals

Lagostrophus fasciatus (Péron). Banded Hare-wallaby.—This species was first described by Péron in 1807. He reported it as being very common on Dirk Hartog as well as on Bernier

and Dorre Islands. It is presumably the wallaby seen by William Dampier in 1699 (Dampier 1729, p. 85).

L. fasciatus is known only from the South west of Western Australia and its northern limit is Bernier Island. To-day there is little doubt that this species is extinct on Dirk Hartog as well as on the mainland. It survives only on Bernier and Dorre Islands. Local knowledge from the Shark Bay area puts the date of extinction of the "wallabies" (possibly including the two species below) in the 1920s. It must have been some time ago since we did not locate any skeletal remains. It is perhaps pertinent that Shortridge (1909, p. 818) stated that "... in the south of Dirk Hartog there is a large sheep station and the wallabies are said to have entirely left that end of the island".

Following our 1972 visit the Western Australian Wildlife Authority and Sir Thomas Wardle agreed on a programme, to be carried out by the Western Australian Wildlife Research Centre, to attempt the re-introduction of the Banded Hare-wallaby to Dirk Hartog Island. In April 1974 11 adult animals (4 male, 7 female, 6 with small pouch young) which had been captured on Dorre Island were placed in two pens on Dirk Hartog. By December, 1976, the breeding colony had increased to 33 adults and 3 dependent young. An attempt to reduce feral cat numbers (see below) is under way, and the first releases of wallabies to the wild took place during May 1977.

Knowledge of the biology of *Lagostrophus* is summarised by Ride and Tyndale-Biscoe (in Ride *et al.* 1962) and Tyndale-Biscoe (1965).

Lagorchestes hirsutus (Gould). Western Hare-wallaby.—This wallaby occurs on Bernier and Dorre Islands but is very rare on the mainland. While some authors have noted that it occurred or probably occurred on Dirk Hartog (e.g. Shortridge 1909; Glauert 1933; Main 1961; Main and Yadav 1971) it appears that no specimen has been collected and some doubt must remain that it ever existed there.

Bettongia lesueur (Quoy & Gaimard). Boodie.—The Boodie was first collected as a skull picked up on Dirk Hartog by Freycinet's Expedition (Quoy and Gaimard 1824). They obtained no entire animals but caught glimpses of an animal that lived in burrows and foraged in the debris on the beaches at night. This description fits that of *B. lesueur*, but not of any of the hare wallabies. No specimen has since been collected on Dirk Hartog.

The Boodie once had a wide distribution in the southern two thirds of Australia. It appears to be extinct on the mainland and is now confined to Barrow, Boodie (a small island south of Barrow), Bernier and Dorre Islands. We saw no sign of it during our visits.

Peramelus bougainville (Quoy & Gaimard). Marl.—This bandicoot is common on Bernier and Dorre Islands, but has not been collected on Dirk Hartog. It was first collected on Peron Peninsula by Quoy and Gaimard and the Western Australian Museum has a single specimen

from Onslow which was collected in 1909. The only possible reference to this species on Dirk Hartog is the sighting of a "small opossum" on the island by A. C. Cunningham, the botanist with King's expedition in 1821 (King 1827). This has been interpreted by Alexander (1915, p. 123) as being a reference to *Perameles bougainville*. We saw no evidence of it during our visit.

Pseudomys hermannsburgensis (Waite). Sandy Mouse.—Nine specimens have been taken from the island. Four were from a trapline located 10 km south of the homestead. This area consists of deep white sand with occasional limestone outcrops and the vegetation is an *Acacia* low shrubland mixed with spinifex (*Plecottrachne* sp.). One was from an *Acacia* thicket at the base of a dune 13 km south of the homestead. Two came from red sand near Sandy Point outcamp where the vegetation is a tall shrubland of *Acacia ligulata*, *Alyogyne cuneiformis* and *Thryptomene baeckeacea* with spinifex (*Plecottrachne* sp.) as a scattered ground cover. One specimen from Sandy Point was taken during September 1972, the remainder in April 1974. A. G. Wells collected two specimens at Herald Bay in September 1973. The species has not previously been recorded from Dirk Hartog. It has a wide distribution in the dry parts of the interior (Ride 1970) and is also known from Rosemary Island (Burbridge and Prince 1972).

Pseudomys albocinctus (Gould). Ashy-grey Mouse.—Two specimens were taken, both in April 1974, at a location 10 km south of Dirk Hartog homestead. The soil and vegetation are described above under *P. hermannsburgensis*. This species was also previously unknown from Dirk Hartog. It occurs on Bernier and Dorre Islands, and on the mainland in various sandplain habitats in the south-west.

Mus musculus (Linnaeus). House Mouse.—Nine specimens have been collected, two in September 1972 and the remainder in April 1974. This species was present in all habitats which were trapped and occurs commonly around the homestead.

Nyctophilus goffroyi (Leach). Lesser Long-eared Bat.—In September 1972, one specimen was captured by hand as it was flying out of a cave in the cliffs on the western side of the island near West Coast Mill. The species has a wide distribution.

Eptesicus pumilis (Gray). Little Bat.—Two specimens were taken in April 1974. One was collected at Sandy Point Outcamp and the other in a cave near West Coast Mill. The species has a wide distribution.

Capra hircus (Linnaeus). Goat.—We saw about 140 goats during the 1972 visit. Four flocks were seen; one of 56, one of about 50 and two of 20. At the time station hands estimated that there were about 700 goats on the island. Our observations suggest that this figure may be conservative.

The domestic goat turned feral is now a common animal in many parts of Western Australia and the damage which it is doing to the

vegetation is only beginning to be appreciated by pastoralists and the general public. On Bernier Island goats were introduced in 1899 and extensive damage has been done to the vegetation. Air photographs show that the number and extent of sand dune blowouts have increased greatly over the past 20 years. Following the recommendations of a party of scientists who visited the island in 1959 (Ride *et al.* 1962) the Department of Fisheries and Wildlife carried out a campaign of attack on the goats and by 1972 more than 450 had been shot. We estimate that at the commencement of shooting in 1959 Bernier Island carried about 350 goats, or 1 goat to 12 ha. With a similar density Dirk Hartog could support a population of about 5 000.

However, on Dirk Hartog goat density is affected by two factors not present on Bernier. These are the presence of drinking troughs which may allow an even greater density, and competition for food from sheep. Sheep numbers in the past have been over 10 000 (see below) and this may have kept goat numbers down. However, goats tend to browse shrubs much more than do sheep and would not always be in direct competition for food.

Damage to vegetation by sheep and goats on Dirk Hartog was obvious but it did not appear to be worse than that on Bernier Island except where heavy overgrazing had occurred near drinking troughs.

Following the 1972 visit we voiced our concern about goats to Sir Thomas Wardle and he responded by placing a bounty on them. About 800 were destroyed during the following two years.

Ovis aries (Linnaeus). Sheep.—Dirk Hartog has been used as a sheep station since 1899. The number of sheep on the island has usually been between 10 000 and 11 000. In 1972 the population was only about 4 000 and only the southern two-thirds of the island was stocked.

Equus caballus (Linnaeus). Horse.—During our 1972 visit we were told that there were about 12 horses on the island, all mares.

Camelus dromedarius (Linnaeus). Camel.—Carter (1917) records that during his visit camels were used to take rations to men stationed at outcamps and windmills. There are no camels on the island at present.

Felis catus (Linnaeus). Domestic Cat.—The domestic cat is well established on Dirk Hartog. Although sightings of the animal itself were infrequent, tracks were seen all over the island.

It is not known when the species became established but it seems probable that cats were taken to the island when the sheep station was established. Carter (1917, p. 605) states that 'cats . . . are now becoming numerous on the island'.

Feral cats are common and widespread on the Australian mainland. They are also known from three other islands off the west coast—Trimouille and Hermite islands in the Monte Bello group and Rottnest Island near Perth. On Hermite

they have apparently been responsible for the disappearance of two species of marsupials and two species of birds (Burbidge 1971). These are the Spectacled Hare-wallaby (*Lagorchestes conspicillatus*), Golden Bandicoot (*Isodon auratus*), Black and White Wren (*Malurus leucopterus*) and Spinifex-bird (*Eremiornis carteri*). On Rottnest Island the cats have been reduced in number by poisoning programmes.

Two cats shot near the homestead in April 1974 had a variety of materials in their stomachs. In both a large centipede predominated but one had the remains of a Zebra Finch and the gecko *Gehyra variegata* while the other contained remains of a Silver Gull.

Dugong dugon (Lacépède). Dugong.—Shark Bay is considered to be the southern limit of the range of this species on the west coast, although occasional animals have been sighted further south, for example off Geraldton. On 3 September 1972, we saw between 30 and 40 Dugong feeding in shallow water adjacent to Quoin Bluff South. One or two are often seen near the homestead.

Neophoca cinerea (Péron & Lesueur). Australian Sea Lion.—King (1827) records that Cunningham, the botanist accompanying his expedition, saw a Sea Lion on Dirk Hartog Island in 1821. Local knowledge indicates that this species is occasionally found in Shark Bay, although the northern limit of its distribution is usually the Abrolhos Islands.

Mammalian Sub-fossil Material.—Because of the lack of evidence regarding the presence of *Lagorchestes hirsutus* and *Perameles bougainville* we arranged for Dr D. Merrilees and Mr A. Baynes of the Western Australian Museum to visit the island and collect sub-fossil material. During a short visit in April 1974 they excavated cave deposits at Herald Heights and Notch Point with the following results (Merrilees and Baynes, pers. comm.).

Herald Heights

Sminthopsis cf. *murina*
Antechinus apicalis
Dasycercus cristicauda
Perameles bougainville
Bettongia lesueur
Bettongia penicillata
Leporillus conditor
Pseudomys hermannsburgensis
Pseudomys shortridgei
Pseudomys praeconis
Pseudomys sp.

Notch Point

Dasyurus geoffroyi
Perameles bougainville
Bettongia lesueur
 cf. *Pseudomys praeconis*

The *Pseudomys* sp. from Herald Heights is not *P. albocinereus* but is larger and might be *P. desertor*. It can be seen that although *Perameles* did occur on Dirk Hartog at some time the deposits did not yield remains of *Lagorchestes*. This does not prove that *Lagorchestes* did not

occur there. With the exception of the *Bettongia* spp., all the above are comparatively small animals and the deposits may have been accumulated by owls or other similar-sized predators. *Bettongia lesueur* live in burrows and could have made their own way into these caves. There are no *Lagostrophus* in the deposits, and it and the similarly sized *Lagorchestes* may have been too large to be taken by the predator concerned.

In April 1974, W. K. Youngson found what appeared to be the sub-fossil remains of an owl pellet deposit in a cave near the ocean adjacent to West Coast Mill. This deposit contained remains from the following species: *Perameles bougainville*, *Dasyurus geoffroyi*, *Dasyercus cristicauda*, *Sminthopsis cf. murina*, *Leporillus concolor*, *Pseudomys hermannsburgensis*, *P. praeconis*, *P. shortridgei* and *Nyctophilus geoffroyi*.

Birds

Observations on the birds of Dirk Hartog Island have been the subject of a number of publications over the years, including Carter (1917, 1923), Whitlock (1921), Ashby (1927),

Sedgwick (1968), Wells and Wells (1974) and Davies and Chapman (1975). The last of these provides a comprehensive summary of the observations of previous authors and lists some 77 species for the island, four of which are seabirds listed as "off Dirk Hartog". To this we can add 7 species—*Anas gibberifrons* (Grey Teal), *Tringa brevipes* (Grey-tailed Tattler) seen in April 1972, *Nymphicus hollandicus* (Cockatiel) seen in April 1974, *Calidris canutus* (Knot), *Sterna dougallii* (Roseate Tern), *S. bengalensis* (Lesser Crested Tern) and *Cheramoea leucosternum* (White-backed Swallow) seen in December 1976. Tattlers were also plentiful at the time of this visit. We also observed a single Rock Dove or Domestic Pigeon (*Columba livia*) on the island in 1972. This was a stray racing pigeon, carrying a Pigeon Racing Federation band. Wells and Wells (1974) recorded another racing pigeon in 1973. From Davies and Chapman's Appendix 5—Species not seen since 1921—we can remove Large Sand Dotterel (seen in 1972 and 1976), Greenshank (1974 and 1976), Bar-tailed Godwit (1972 and 1976) and Little Wood Swallow (1972).

* <i>Pelecanus conspicillatus</i>	Australian Pelican	* <i>Sterna bergii</i>	Crested Tern
* <i>Phalacrocorax varius</i>	Pied Cormorant	† <i>Sterna bengalensis</i>	Lesser Crested Tern
* <i>Egretta sacra</i>	Reef Heron	<i>Geopelia cuneata</i>	Diamond Dove
† <i>Tadorna tadornoides</i>	Mountain Duck	<i>Phaps chalceptera</i>	Common Bronzewing
* <i>Anas gibberifrons</i>	Grey Teal	<i>Cacatua sanguinea</i>	Little Corella
<i>Accipiter fasciatus</i>	Australian Goshawk	<i>Cacatua roseicapilla</i>	Galah
* <i>Accipiter cirrocephalus</i>	Collared Sparrowhawk	† <i>Nymphicus hollandicus</i>	Cockatiel
* <i>Aquila audax</i>	Wedge-tailed Eagle	<i>Neophema pectorifila</i>	Rock Parrot
* <i>Hieraaetus morphnoides</i>	Australian Little Eagle	<i>Cuculus pallidus</i>	Pallid Cuckoo
* <i>Haliaeetus leucogaster</i>	White-breasted Sea Eagle	<i>Chrysococcyx basalis</i>	Horsfield Bronze Cuckoo
<i>Circus assimilis</i>	Spotted Harrier	<i>Ninox novaeseelandiae</i>	Boobook Owl
* <i>Pandion haliaetus</i>	Osprey	<i>Eurostopodus guttatus</i>	Spotted Nightjar
* <i>Falco cenchroides</i>	Nankeen Kestrel	† <i>Cheramoea leucosternum</i>	White-backed Swallow
<i>Falco berigora</i>	Brown Falcon	* <i>Hirunda neoxena</i>	Welcome Swallow
<i>Turnix varia</i>	Painted Quail	<i>Petrochelidon nigricans</i>	Tree Martin
<i>Rallus philippensis</i>	Banded Landrail	* <i>Anthus novaeseelandiae</i>	Australian Pipit
* <i>Eupodotis australis</i>	Australian Bustard	<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-Shrike
* <i>Haematopus ostralegus</i>	Pied Oystercatcher	<i>Cincloramphus cruralis</i>	Brown Songlark
* <i>Haematopus fuliginosus</i>	Sooty Oystercatcher	* <i>Malurus leucopterus</i>	Black-and-white Wren
* <i>Vanellus tricolor</i>	Banded Plover	* <i>Malurus lamberti</i>	Variegated Wren
<i>Peltohyas australis</i>	Australian Dotterel	* <i>Stipiturus malachurus</i>	Southern Emu-Wren
* <i>Charadrius alexandrinus</i>	Red-capped Dotterel	* <i>Sericornis maculatus</i>	Spotted Scrub-Wren
* <i>Charadrius leschenaulti</i>	Large Sand Dotterel	* <i>Calamanthus fuliginosus</i>	Field-Wren
† <i>Pluvialis squatarola</i>	Grey Plover	<i>Amytornis textilis</i>	Western Grass-Wren
* <i>Arenaria interpres</i>	Turnstone	* <i>Ephthianura albifrons</i>	White-fronted Chat
† <i>Numenius phaeopus</i>	Whimbrel	<i>Ephthianura tricolor</i>	Crimson Chat
† <i>Numenius madagascariensis</i>	Eastern Curlew	<i>Petroica goodenovii</i>	Red-capped Robin
† <i>Tringa nebularia</i>	Greenshank	<i>Petroica cucullata</i>	Hooded Robin
<i>Tringa hypoleucos</i>	Common Sandpiper	* <i>Rhipidura leucophrys</i>	Willie Wagtail
* <i>Tringa brevipes</i>	Grey-tailed Tattler	<i>Oreocica gutturalis</i>	Crested Bell-Bird
† <i>Calidris canutus</i>	Knot	<i>Dicaeum hirundinaceum</i>	Mistletoe Bird
* <i>Calidris acuminata</i>	Sharp-tailed Sandpiper	* <i>Zosterops gouldi</i>	Western Silvercyc
* <i>Calidris ruficollis</i>	Red-necked Stint	<i>Lichmera indistincta</i>	Brown Honeyeater
* <i>Limosa lapponica</i>	Bar-tailed Godwit	* <i>Meliphaga virescens</i>	Singing Honeyeater
* <i>Himantopus himantopus</i>	White-headed Stilt	* <i>Poephila guttata</i>	Zebra Finch
* <i>Burhinus magnirostris</i>	Southern Stone-Curlew	<i>Grallina cyanolucca</i>	Magpie-Lark
* <i>Larus pacificus</i>	Pacific Gull	* <i>Artamus cinereus</i>	Black-faced Wood-Swallow
* <i>Larus novaehollandiae</i>	Silver Gull	* <i>Artamus minor</i>	Little Wood-Swallow
* <i>Hydroprogne caspia</i>	Caspian Tern	* <i>Cracticus torquatus</i>	Grey Butcher-Bird
† <i>Sterna dougallii</i>	Roseate Tern	* <i>Corvus bennetti</i>	Little Crow
<i>Sterna nereis</i>	Fairy Tern		

A full list of those species known from the island follows. Those birds observed by us in 1972 are marked with an asterisk and additional species seen by us since 1972 with a dagger.

The avifauna of Dirk Hartog Island does not comprise a large number of species but it does show some interesting differences from that of Peron Peninsula, immediately to the east. Wrens are much more common on the island. Indeed Carter (1917, p. 571) suggested that "Dirk Hartog might be called an island of Wrens, as at least ninety of every hundred land-birds seen are Wrens". On the other hand a number of common arid zone species which occur on Peron Peninsula are uncommon or absent on the island, e.g. Crested Pigeon, Wedgebill, Pallid Cuckoo and Crested Bell-Bird. Davies and Chapman (1975) suggest that this could be due to some species having only recently arrived in the area. It could also be due to the difference in soils and vegetation—Peron Peninsula has a vegetation similar to much of the Murchison (Beard 1976) while Dirk Hartog has no Bowgada (*Acacia ramulosa*) and has a less dense shrub layer and more heath-like formations. Dirk Hartog's avifauna will probably prove to be more akin to the mainland south of the island (Edel Land) which has a similar vegetation.

Most species recorded from Dirk Hartog have wide-ranging distributions and many, e.g. the Zebra Finch, Little Crow and Little Wood-Swallow are typical of the arid zone. However, two southern species, the Rock Parrot and the Southern Emu-Wren occur here at the northern end of their range. The Spotted Scrub-Wren extends northward only as far as Bernier and Dorre Islands. Other species close to the northern end of their range are the Western Silvereye and White-fronted Chat. The Black-and-white Wren is of special interest, being restricted to Dirk Hartog and Barrow Islands.

On 3 September 1972 we inspected the nesting colony of Pied Cormorants at Quoin Bluff South. We estimated the number of nests at about 2 500, the same figure reached by Whitlock in 1920. Only about 1% contained eggs; most contained half grown young.

Other birds which were breeding during this visit included Grey Teal (young almost fully fledged), Nankeen Kestrel (eggs), Caspian Tern (one nest with 2 eggs on Cape Ransonnet), Crested Tern (one chick on Meade Island), White-breasted Sea Eagle (a chick in a nest at Quoin Bluff South), Osprey (several nests, both eggs and chicks present), Banded Plover (a nest at Two Wells Mill, one young almost fully fledged near Bottom Ten Mile Mill) and Little Crow (several nests; one we inspected had 6 eggs, another at Cape Inscription had newly hatched chicks).

On 9 December 1976 we found a Roseate Tern colony of between 200 and 300 nests on the northern tip of Meade Island which is adjacent to the Homestead and joined to Dirk Hartog Island at low tide. Most nests had one egg, 2 to 3% had two eggs and in about 5% the eggs

had recently hatched. Over 500 terns were sighted in the vicinity; between 5 and 10% were in juvenile plumage.

Reptiles

The following species have been collected from Dirk Hartog Island and specimens are lodged in the Western Australian Museum.

GEKKONIDAE

Crenadactylus ocellatus horni (Lucas & Frost)
Diplodactylus spinigerus Gray
Diplodactylus vittatus Gray
Gehyra variegata (Duméril & Bibron)
Heteronotia binocci (Gray)
Nephurus levis occidentalis Storr
Phyllurus mili Bory

PYGOPODIDAE

Delma nasuta Kluge
Lialis burtonis Gray
Pygopus lepidopodus (Lacépède)

AGAMIDAE

Amphibolurus maculatus maculatus Gray
Amphibolurus minor Sternfeld
Amphibolurus parviceps (Storr)
Amphibolurus reticulatus (Gray)

SCINCIDAE

Cryptoblepharus carnabyi Storr
Ctenotus fallens Storr
Ctenotus lesueurii (Duméril & Bibron)
Ctenotus youngsoni Storr
Egernia stokesii badia Storr
Lerista elegans (Gray)
Morethia lineocellata (Duméril & Bibron)
Lerista lineopunctulata (Duméril & Bibron)
Lerista praepedita (Boulenger)
Omolepida branchialis (Günther)
Tiliqua rugosa (Gray)

VARANIDAE

Varanus gouldii (Gray)

ELAPIDAE

Demansia olivacea (Gray)
Demansia reticulata (Gray)
Pseudechis australis (Gray)
Vermicella littoralis Storr

HYDROPHIIDAE

Hydrophis elegans (Gray)
Hydrophis major (Shaw)

Ours were the first extensive collections of reptiles made on Dirk Hartog Island. In general the species present are typical of the warmer and drier parts of south-western Australia. The only northern element is the gecko *Nephurus levis*, which, however, extends as far south as Geraldton.

The skink *Ctenotus youngsoni* is restricted to the Shark Bay area, being known only from Dirk Hartog and the northern part of Edel Land.

Invertebrates

No systematic collecting of invertebrates was attempted. On 29 April 1974, W. K. Youngson collected a sample of humic soil from near Sandy Point from which five species of land snail were obtained. These were *Westralaoma* sp., *Themapupa* sp., *Australbinula* sp., *Austrosuccinea* sp. and *Bothriembryon* sp. Publications on invertebrates from Dirk Hartog include Ashby (1929), Hale (1929) and Allender (1969).

Acknowledgements.—We are most grateful to Sir Thomas Wardle, the lessee of Dirk Hartog Station, for inviting us to visit the island and for assisting us in many ways. Our thanks also go to Dr. G. M. Storr and Mr. A. Baynes of the Western Australian Museum for identifying the reptile collection and the *Pseudomys* respectively. Assistance in determining plants was received from Professor and Mrs. D. G. Carr, Australian National University (*Eucalyptus*); Dr. H. J. Eichler, Herbarium Australiense (*Neosciadium*); Mr. D. Hassall, University of Queensland (*Euphorbia*, *Chamaesyce*); Mr. T. Macfarlane, Australian National University (*Anguillaria*); Mr. D. McGillivray, National Herbarium of New South Wales (*Grevillea*); Mr. B. R. Maslin, Western Australian Herbarium (*Acacia*); Dr. D. E. Symon, Waite Institute (*Solanum*); and Mr. P. G. Wilson, Western Australian Herbarium (*Chenopodiaceae* and *Asteraceae*). Finally we are very appreciative of the pleasant companionship and assistance of Mr. T. Evans and Mr. W. K. Youngson who collected many of the specimens. Our thanks also go to Mr. P. Fuller who assisted during the 1976 visit.

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New data on the origin and distribution of Western Australian sand fulgurites

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Manuscript received 26 July 1977; accepted 23 August 1977

Abstract

Lechatelierite fragments totalling 1 084 g, part of a large sand fulgurite, have been recovered from Black Point, Western Australia. Black to very dark brown, altered, woody material plugged the lumen of many tubular fragments when collected. Finely macerated woody material from the fulgurite shows fibrous and cellular structure under the microscope, is anisotropic, and brown to orange. The mean refractive index of the woody material ranges from 1.574 ± 0.002 to 1.598 ± 0.002 , but most of it is close to 1.579 ± 0.002 . The evidence indicates that the Black Point fulgurite formed around a root. Whether this is a common mode of formation for fulgurites is still open to question, for roots are not necessary for the development of the tubular shape typical of fulgurites.

Lechatelierite tubes are also recorded from west Willetton in the Perth Metropolitan Area, and Mica Hill near Manjimup.

Sand fulgurites have now been recorded from the north of Western Australia almost to its extreme south, but their apparent concentration in the south-west is probably a function of population distribution. Fulgurites are likely to be found in all sandy desert areas of Western Australia, particularly in the north where lightning frequency is high.

Introduction

Sand fulgurites have been recorded from numerous localities in Western Australia, particularly in the south-west (Simpson 1931; Glover 1974, 1975). Most Western Australian fulgurites are represented by a few small fragments of lechatelierite (silica glass) and some by only one piece. Larger collections have been made in the Perth Metropolitan Area from Willetton (500 fragments, totalling about 100 g) and Beechboro (250 fragments, 92 g). The recent recovery of a fulgurite from Black Point (Fig. 1) is of special interest because it is made up of many large tubes containing altered woody material, evidently the remains of a pre-existing root. The possibility that sand fulgurites have formed around roots has been considered by several authors (Lewis 1936, Fenner 1949, Schonland 1964, Trendall 1964) but undoubted field evidence of genetic association has not been adduced. Another point of interest about the fulgurite from Black Point is the large weight of lechatelierite recovered, 1 084 g.

Fulgurite tubes from two other localities, namely west Willetton, and Mica Hill, near Manjimup, are recorded.

Lechatelierite from the Black Point fulgurite is stored in the Western Australian Museum (Nos. G13408 to G13410 inclusive) and the

Geology Department, University of Western Australia (Nos. 84672 to 84675 inclusive). Woody material from the Black Point fulgurite (No. 82871) and lechatelierite from the west Willetton fulgurite (No. 82872) are stored in the Geology Department, University of Western Australia.

The Black Point fulgurite

Microscopic appearance

The Black Point fulgurite was found on 20 March 1977 by Mr George Gardner, Mrs Linda Ronk and Mr Alan Ronk near the western edge of a sand blow-out 1 km north-east of Black Point (Pemberton 1:250 000 map, Series R502, S1 50-10, co-ordinates 354749). When in place it consisted of a fragmented tubular body branching downward into five main off-shoots which decreased in diameter with depth. The branches ended 4 or 5 cm below the waterlogged sand, that is, a little more than 1 m below the surface.

A few fragments from the tops of the branches are quite large. One flattened tubular piece with prominent flanges roughly parallel to its length is 20.5 cm long, up to 6.5 cm wide and about 1.5 cm thick (Fig. 2, left). Other fragments are not flattened in one plane, but are twisted rather irregularly (Fig. 2, right). Frag-

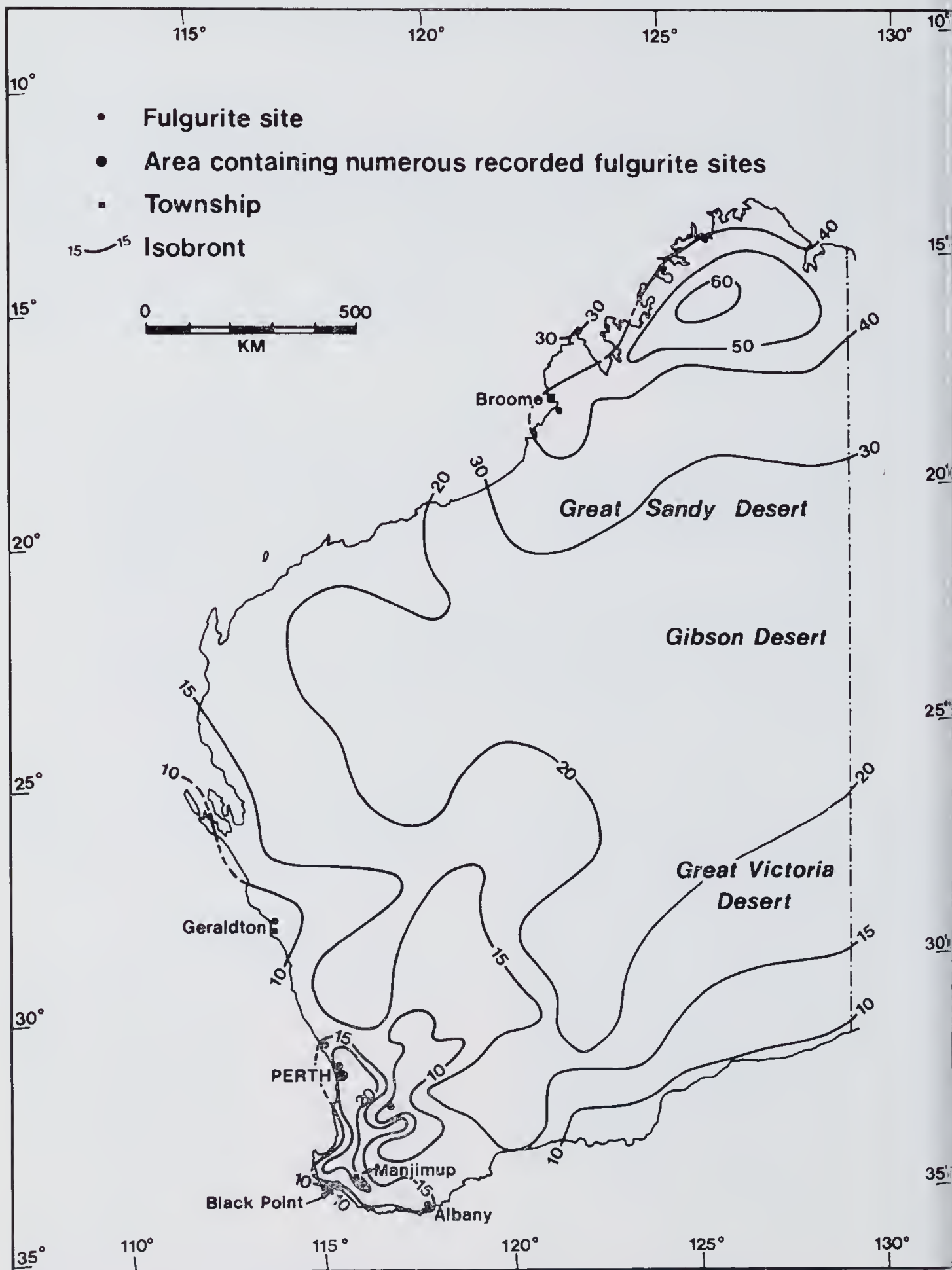


Figure 1.—Average annual thunder day map of Western Australia showing fulgurite sites. The large solid circle around Perth includes 9 separate fulgurite sites, and it is evident that fulgurite recovery is related to population density, and does not reflect the probable distribution of fulgurites. Isobronts after Commonwealth Bureau of Meteorology (1967).



Figure 2.—Two large fragments from the top of the Black Point fulgurite. The fragment on the left is highly flanged, and is flattened in the plane of the photograph. The fragment on the right is flattened in several planes, as though twisted. Scale in cm.



Figure 3.—Fragile fragment from the bottom of a branch of the Black Point fulgurite. Scale in cm.

ments from near the end of branches are thin and fragile, with numerous projections (Fig. 3). The inside of the tube, known as the lumen, is up to 1 cm in diameter in large fragments (Fig. 1), but is commonly flattened or triangular in cross-section. The tube walls of lechatellierite range from about 0.5 to 1 mm in thickness.

The rough, dull, outer surface of the fragments is made up of sand grains embedded in the glass, and contrasts with the shiny, smooth and somewhat mammilated glass on the inside. The outer surface ranges from very light grey (N8) to medium dark grey (N4), but is generally very light grey to light grey (N7) (See Rock-color Chart Committee 1963 for colour terms and accompanying numerical designation). Locally, the outer surface has orange or brownish hues, and material from the water-clogged section is mainly very pale orange (10YR8/2) to pale yellowish brown (10YR6/2). The colour of the inner surface ranges from light grey (N7) to black (N1). The black or dark portions of the glass are irregularly shaped, range from less than 1 mm to several mm in diameter, and constitute about 30% of the glass. They commonly merge insensibly into the light grey glass.

Microscopic appearance

Under the microscope most of the lechatellierite is colourless but there are irregularly shaped brown portions corresponding to the black material of the hand-specimen. The refractive index of the colourless glass is between 1.459 and 1.464 ± 0.002 , and is generally close to 1.461 ± 0.002 . Brown glass is commonly higher in refractive index, and some of the light brown (5YR6/4) glass is about 1.467 ± 0.002 . A few small, intensely coloured portions are harder to measure, but their index is higher still, and seems close to 1.475. Colourless and brown glass are both highly vesicular, with bubbles from 0.01 to 0.3 mm in diameter.

Sand grains embedded in the outer surface of the fulgurite are commonly partly coated with opaque mineral, apparently mainly iron oxide. Many grains are partly converted to glass: they are highly cracked on the outside, and commonly pass, via an altered, brownish, finely fibrous portion, into the glass of the fulgurite wall. This texture shows clearly that the fulgurite formed from fusion of sand grains.

Chemistry

The fulgurite contains little carbon, and a total carbon analysis by combustion on 1 g showed 0.01% C.



Figure 4.—Surface fragment of the Black Point fulgurite showing the lumen. Note the contrast between the smooth, shiny, black and grey inner surface, and the rough, dull, grey, exterior. Scale in cm.

Two black and two colourless portions of glass were analysed with the electron microprobe for SiO_2 , TiO_2 , Al_2O_3 , FeO , MgO , CaO and K_2O . One of the black portions recorded 1.93% TiO_2 and 0.66% FeO , and the other 0.14% FeO . Apart from SiO_2 , which virtually composes the remainder of the dark material, and forms practically 100% of the clear portions, no other oxide is present in more than trace amount.

Part of the fulgurite was crushed, and separated as far as possible by handpicking into dark and light portions. The separated portions were analysed by fusion (the method of Norrish and Hutton 1969) and comparison by XRF with USGS standards. Results for titanium and iron are as follows:

	$\text{TiO}_2\%$	$\text{FeO}\%$
Dark material	0.226	0.218
Light material	0.097	0.279

The combined microprobe and XRF results show that some dark areas are significantly enriched in TiO_2 , but the distribution and role of iron is uncertain. In general, the chemistry indicated by these partial analyses accords with what might be expected from Table 1, which shows that sand near the bottom of the fulgurite is mainly quartz (about 99.4%) with about 0.4% of the titanium-rich heavy minerals ilmenite and leucoxene.

Altered woody material

Sand and altered woody material were found in the lumen of tubes from all parts of the fulgurite. About 7 g of black to dusky brown (5YR2/2) woody matter were recovered for examination. A few of the pieces are 1 cm or more long and over 0.5 cm wide, and plugged the part of the lumen they occupied. They are unlikely to have fallen in, and therefore apparently preceded the fulgurite. The material is partly soluble in weak alkali, giving a brown supernatant liquid indicating the presence of humic acids.

Macerated woody material examined in oils under the polarizing microscope ranges from black and opaque, where coarse, through moderate reddish brown (10R4/6) to yellowish orange (10YR7/6) where sufficiently fine. Elongate fragments are commonly fibrous or have rather irregular structure, and some fragments are fairly homogeneous in appearance. A few pieces show well-developed cells from 8-13 μm in diameter, the cell walls being 1-1.5 μm thick. The material is anisotropic with low birefringence, and ranges in mean refractive index between 1.574 and 1.598 ± 0.002 , with most readings in the narrow interval between 1.575 and 1.583 ± 0.002 . These figures are toward the lower part of the range of 1.55-1.75 found by Pflug (1954) for lignite humites, and taken together with the presence of humic acids, seem to put the material near the peat-lignite boundary.

Petrography of surrounding sand

A sample of sand from around the bottom of the fulgurite was sieved and weighed. The sand is medium-grained ($M=0.28\text{ mm}$), fairly well sorted ($So=1.37$), and consists mainly of quartz. Most grains near the median size are rounded, according to the terminology of Pettijohn (1975, p. 57).

About 95% of the quartz grains are clear, the remainder being cloudy because of numerous minute indeterminate inclusions. Some of the clear grains contain inclusions of opaque mineral, zircon, or tourmaline. The mineral weight % of the sand, obtained from combining grain counts of the weighed size fractions and separated heavy minerals, is shown in Table 1. Three hundred grains from each fraction were counted. Heavy minerals, of which ilmenite is the main constituent, make up only 0.4% of the sand.

Table 1

Weight % of minerals in sand near the bottom of the Black Point fulgurite

Mineral	Weight %
Quartz	99.38
Ilmenite	0.35
Kaolinized feldspar	0.20
Leucoxene	0.03
Zircon	0.02
Magnetite	0.01
Rutile	Trace
Sillimanite	Trace
Kyanite	Trace
Tourmaline	Trace
Staurolite	Trace
Unknown	Trace

The west Willetton fulgurite

The west Willetton fulgurite was found by Mr R. H. Stranger in a road cutting through sand along Agin Court Drive (Pinjarra 1:250 000 map, series R 502 51 50-2, coordinates 386035). It is a tube 3.0 cm long, with an irregularly shaped, very roughly circular cross-section, ranging in diameter from 0.9 mm to 1.3 mm. Wall thickness ranges from about 0.5 mm to 1.0 mm. The rough, outer surface of the tube is white (N9) to very light grey (N8) and contains embedded, partly fused white sand grains that are commonly rounded and about 0.25 mm in diameter. There are no prominent flanges. The surface of the lumen is shiny, fairly smooth to somewhat mammillated, and very light grey. About 20 small, irregularly shaped black portions up to 1 mm in diameter are scattered throughout the wall. The refractive index of the very light grey glass is 1.461 ± 0.002 .

The Manjimup fulgurite

The Manjimup fulgurite is recorded here to correct a published error of location. The fulgurite, CSIRO No. 9073, is a tube with an unusual lacy texture, and was submitted as coming from Wanneroo about 25 km north of Perth. It has already been described and illustrated (Glover 1975, p. 57). The object is now stated by W. M. McArthur (pers. comm. 1976) to have come from a sandpit at Mica Hill, about 14 km south-east of Manjimup, lat. $34^{\circ}19'S$, long. $116^{\circ}12'E$.

The origin of fulgurite morphology

The origin of lechatelierite previously found in sandy areas of Western Australia has been attributed to fusion of the sand by lightning (Glover 1974). The full argument will not be repeated here. It is enough to say that there are two Australian reports of sand fulgurites collected after observed lightning strikes (Simpson 1931, Fenner 1949, p. 128), and numerous extra-Australian reports (see for example Pfaff 1822, Wicke 1859, Van Bastelaer 1883, Diller 1884, Bayley 1892, Wood 1910, Noe-Nygaard 1973), and that all Western Australian lechatelierite fragments described have the same morphology and mineralogy as the bodies formed by lightning. All are either tubes, or fragments of tube walls or their flange-like extensions. It is still not clear, however, why sand fulgurites adopt a tubular habit.

Rock fulgurites are not recorded in Australia, and are therefore rather neglected in the local literature. Nevertheless, as they commonly take the form of glass-walled tubes within the rock, they should be considered in any argument about the origin of the tubular shape of sand fulgurites. Rock fulgurites seem to be found mainly on mountain peaks subject to lightning strikes. They have been described in a wide range of rock types, notably hornblende gneiss (Rutley 1885), glaucophane schist (Rutley 1889), and serpentine (Aston and Bonney 1896) from the European Alps; andesite from the San Francisco Peaks, Arizona (Davis and Breed 1968) and Little Ararat, Turkey (Switzer and Melson 1972); quartz diorite porphyry from Crested Butte,

Colorado (Switzer and Melson 1972); hornfels from Castle Peak, Colorado (Switzer and Melson 1972); trachyte from Nevado de Toluca in Mexico (von Humbolt 1845, reported in Davis and Breed 1968); and siliceous limestone from the Pyrenees (Diller 1884). They have even been reported from streets in Detroit (Hill 1947).

The presence of altered woody material within the Black Point fulgurite suggests that lightning followed down a small root and fused surrounding sand to form lechatelierite. The concept that roots have conveyed current in this way is not new, and has been considered for example by Lewis (1936), who described a fulgurite with an internal surface film of carbon, and by Schonland (1964), Fenner (1949) and Trendall (1964). Bushes or shrubs are quite likely to be struck by lightning, and live roots would be a better conductor than surrounding sand. Nevertheless, roots are not necessary for the development of tubular fulgurites. Some artificial fulgurites are tubular (Petty 1936; Fenner 1949; Schonland 1964) and a tubular sand fulgurite was recovered from a heap of building sand after it was struck by lightning (Van Bastelaer 1883). As mentioned above, many rock fulgurites are also tubular. Conventional theory attributes the lumen in sand fulgurites to thermal expansion of air or water, although a supposed mechanical action of the lightning in forcing the sand apart has also been suggested (see Frondel 1962). Vesicles are presumably caused by expanding gas or vapour. The very low amount of carbon in the Black Point fulgurite accords with the hypothesis that the sand was forced away from the root as it fused. Flattening and deformation of the lumen could be brought about by subsequent sand pressure on the plastic glass.

To sum up, the presence of altered woody matter in the Black Point fulgurite seems to be the firmest evidence found so far that a sand fulgurite has formed around a root. Whether this is a common mode of formation for sand fulgurites is still open to question.

Probable distribution of sand fulgurites in Western Australia

Most Western Australian fulgurites have been recorded from the populous south-west of the State, especially around Perth, and this almost certainly reflects the distribution of observers rather than fulgurites. The fulgurites are generally revealed in deflating areas, where wind has blown away sand and left the lechatelierite fragments.

One of the main factors affecting fulgurite abundance is the frequency of lightning, which is indicated cartographically by lines called isobronts that join places with an equal number of thunder-days in a given period. Nevertheless, isobrontic maps have not proved a reliable guide to the abundance of sand fulgurites, and it is worth considering why this may be. Thunder data are probably insufficient in many countries to produce reliable isobrontic maps, and it is notable that satellite data gathered on the world

distribution of some 7 000 lightning strikes in 1969-70 (Sparrow and Ney 1971) can be reconciled with the current isobrontic maps of some areas only in a fairly general way. However, there are certainly other factors. The thunder recorded on the maps includes an indeterminate proportion caused by cloud-to-cloud lightning, which is obviously irrelevant to any consideration of fulgurite formation. The age of the land surfaces, and the consequent period of their exposure to lightning are important, as are pronounced climatic changes in areas with long-exposed surfaces. The surface should be sandy and not shielded by a dense canopy of vegetation. Local conditions in sandy terrains can play a significant part: for example Lacroix (1931, 1942) emphasizes that Saharan fulgurites are only found near the base of dunes, where sand is moister than on the crest. Fulgurites may be less noticeable in some places because sand movement has broken them into small fragments, or because they are concealed under a growing sand cover. Whatever the combination of reasons, classical African fulgurite localities in the Sahara Desert (Lacroix 1931, 1942) and in the Kalahari Desert (Lewis 1936), show an isobrontic range from 40 to less than 10 (isobrontic data from the map of Griffiths 1972, p. 29). There is a similar situation in Western Australia, where recorded fulgurite localities show an isobrontic range from higher than 40 to less than 10 (isobrontic data from Commonwealth Bureau of Meteorology 1967). It seems that most sandy areas in Western Australia will yield fulgurites, and that they may be especially abundant in the thunder-prone northern areas of the Great Sandy Desert (see Fig. 1).

Acknowledgements.—The Black Point fulgurite was forwarded to the Western Australian Museum after careful excavation by G. Gardner, L. Ronk and A. Ronk, and was transmitted for examination to the Geology Department, University of Western Australia, by D. Merrilees. The west Willetton fulgurite was collected by R. H. Stranger. Electron-probe work on the Black Point fulgurite was done by M. J. Gole, and XRF and total carbon analyses by R. Lee.

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Reptilian fossils from Windjana Gorge, Western Australia

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(communicated by P. E. Playford)

Manuscript received 13 December 1976; accepted 26 July 1977

Abstract

A late Cainozoic lag gravel from Windjana Gorge contains the remains of a large crocodile and fragments of at least two chelonian genera. The distinctive ornamentation of some of these latter fragments suggest *Carettochelys*, a genus now restricted to New Guinea and the extreme north-eastern Northern Territory. The age of the fauna is difficult to assess but the presence of re-worked laterite pebbles suggest a post-Miocene age. If the deposit is correlated with the Warrimbah Conglomerate (Veevers & Wells, 1961) the age is no younger than Late Pleistocene.

Introduction

Reptilian fossils were collected from a Cainozoic lag gravel on the north-western face of Windjana Gorge, Western Australia (Fig. 1), during 1972. Other Cainozoic vertebrate remains from the area include *Diprotodon australis*, from the bed of the Lennard River, downstream from Windjana Gorge (Hardman 1884) and large macropodine and crocodilian remains from as well at the "foot of St George Ranges, Cherrapun Station, Fitzroy River" (Merrilees 1968). Blauert (1921) reported crocodilian and marsupial remains from Quanbun Station in rocks thought to be of Pleistocene age. The associated marsupials are *Phascolonus gigas*, a large macropodine resembling *Protemnodon anak* and another large macropodine (Merrilees 1968).

Description of site

The fossils were recovered from a lag conglomerate deposited in, and adjacent to, a shallow cave in the northwest wall of Windjana Gorge, 900 m from the downstream end of the gorge and 41 m above the bed of the Lennard River. The cave is of no speleological significance but is typical of corrosion and solution features developed in vertical limestone cliff faces at or near river level (Jennings & Sweeting 1963, p. 34). The conglomerate is poorly exposed and it is partly covered by limestone talus. As a result, the exact extent of the deposit is difficult to determine, but it is at least 2 m long, 1.5 m wide and 1 m high. The deposit has been partly eroded. The contact between the conglomerate and the limestone is sharp but irregular. Where covered by the conglomerate the surface of the limestone appears to be smooth and resembles similar solution features developed at or just above the present river level. Exposed limestone surfaces are generally marked by rillen-karren structures.

The conglomerate is composed of rounded to subrounded quartz pebbles and subrounded to subangular quartz sand with minor amounts of mica, feldspar, and dark minerals. It contains rounded limestone cobbles as well as a few fragments of speleothem that apparently have fallen from the cliff face. The matrix is composed of limonitic clay and silt particles and part of the deposit is cemented by calcium carbonate. The uncemented portion is very friable but where cemented, fractures frequently break across quartz pebbles rather than around the margins of the pebbles.

Palaeontology

Class Reptilia
Subclass Archosauria
Order Crocodilia
Suborder Eusuchia
Family Crocodylidae
Genus ?*Crocodylus*
?*Crocodylus* sp. indet.

(Fig. 2A, B, C; Fig 3A, C.)

Material studied.—Incomplete left premaxillary fragment (CPC 17122), dermal scutes and fragmentary bones (Figs. 2A, B, C, 3A, C). The crocodilian remains were compared with remains of *Crocodylus porosus* (Fig. 2D) from the Northern Territory, material from Chinchilla and the Darling Downs, Queensland and from sites in Western Australia, cranial and scute remains of *Crocodylus johnsoni* (Fig. 3B) collected from the Lennard River, and illustrated material.

Premaxillary.—The fragmentary premaxillary (Figs. 2A, B, C) is 85 mm across at the widest point and exceeds 100 mm in length. The anterior part is missing and the posterior part is broken off behind the alveolus of the largest tooth. No teeth are in place, but fragments of the largest tooth (maximum diameter anterior-

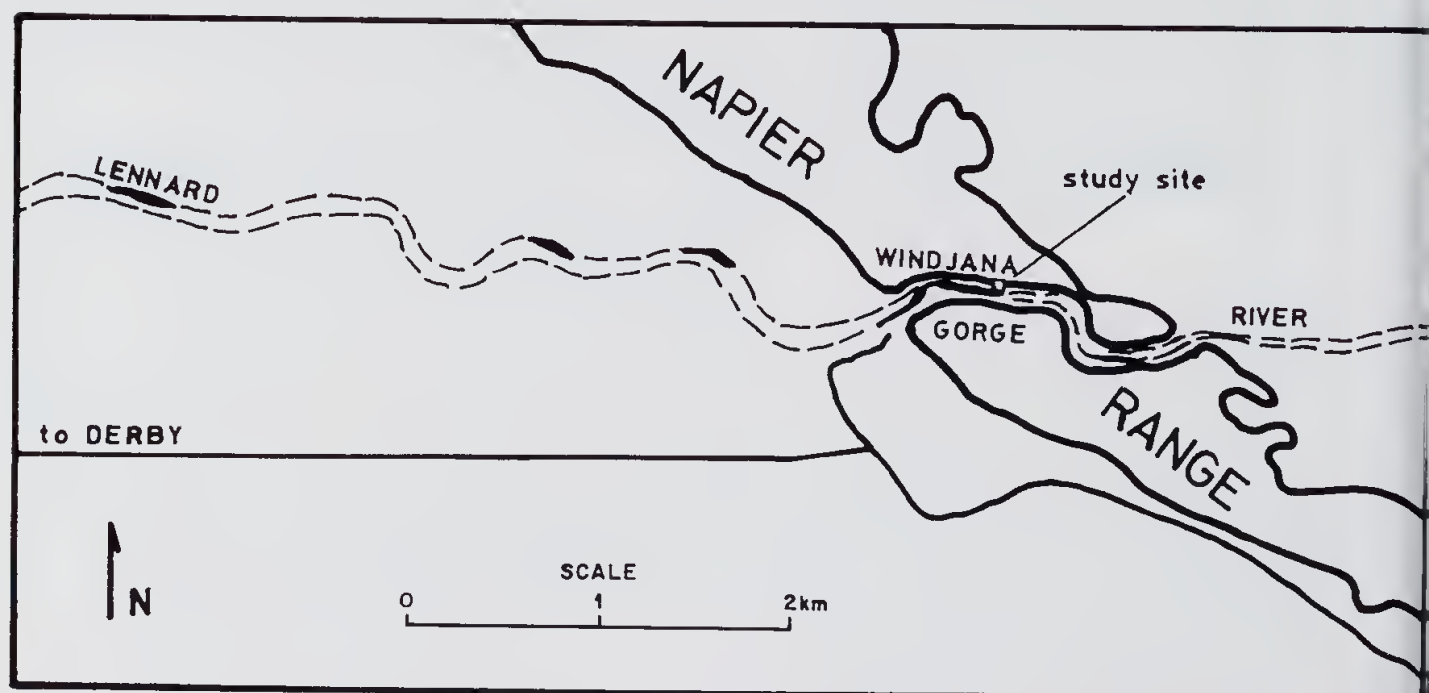


Figure 1.—Locality map showing the study site in Windjana Gorge. After the Lennard River 1:100 000 (Sheet 3863) topographic map.

posterior 29 mm) are cemented to the side of its alveolus. Anterior to the major tooth are alveoli for two more teeth, the posterior being the larger and the anterior being very much reduced. No alveolus is present for the posterior premaxillary tooth as the fossil is broken before the position of this tooth, but the tapering of the raised dental platform suggests that this tooth was very much smaller than the tooth immediately anterior to it. Comparison with the extant *Crocodylus porosus* (Fig. 2D) suggests that a fifth tooth was probably present at the extreme front of the snout just off-centre from the premaxillary suture. Thus the Windjana specimen probably had at least five, and probably no more than six, premaxillary teeth and differs in this respect from *C. porosus*, which has 4 premaxillary teeth (Iordansky 1973). The size differential of the teeth in the Windjana specimen serves to distinguish it from *C. johnsoni*, which has five teeth of similar size in the premaxillary (Woodburne 1967; Longman 1925a). Thus the fossil is distinct from both the extant Australian crocodiles.

The Windjana fossil was then compared to a small sample of fossil crocodilians and illustrated material. A fragmentary right premaxillary (QM F6123) from Chinchilla, Queensland, identified as *Pallimnarchus pollens*, is distinct from the Windjana fossil as the premaxillary probably bore more than six teeth. The Chinchilla specimen has five broken teeth in alveoli and one empty alveolus in the anterior portion; the anterior teeth and front of the premaxillary are missing. The general shapes of the two specimens, suggested by the preserved curvature of the outer surfaces, are distinct. The Windjana form probably possessed a blunter snout (brevirostrine), the outer bone surface curves strongly in front of the second largest tooth and

the smallest tooth socket preserved is labially positioned just anterior of this tooth. Iordansky (1973) indicates that the largest teeth in both the upper and lower jaws lie in the central portions of the convex arches of the undulating jaw margins and reflect the pseudoheterodonty. Thus, conversely, the more marked the tooth size differentiation, the more pronounced the development of notches. In the Chinchilla specimen the line of the premaxillary immediately anterior of the largest tooth flexes slightly inwards but then straightens to run anteriorly, without a pronounced inward curvature; the snout probably tapered more than the Windjana form. The amount of curvature of the anterior part of the premaxillary on the Windjana form is reminiscent of that illustrated by Woodburne (1967 pl. 7 middle) as a probable juvenile right premaxillary of *Crocodylus* sp. from the Miocene and of *P. pollens* from Landsdowne illustrated by Longman (1925b, fig. 1).

The crocodilian described under the cabinet name of *Pallimnarchus pollens* (de Vis 1885) had a distinct premaxillary-maxillary notch similar to that described for *Pallimnarchus pollens* from Landsdowne Station (Longman 1925b). Projection of the snout curvature of the Windjana premaxillary suggests the animal was more allied to the short snouted (brevirostrine) crocodiles than other forms. The marked size differentiation of the premaxillary teeth of the Windjana fossil further suggests the form possessed a premaxillary-maxillary notch (cf. Iordansky 1973, p. 241).

Characteristics of crocodilian premaxillaries are compared in Table 1.

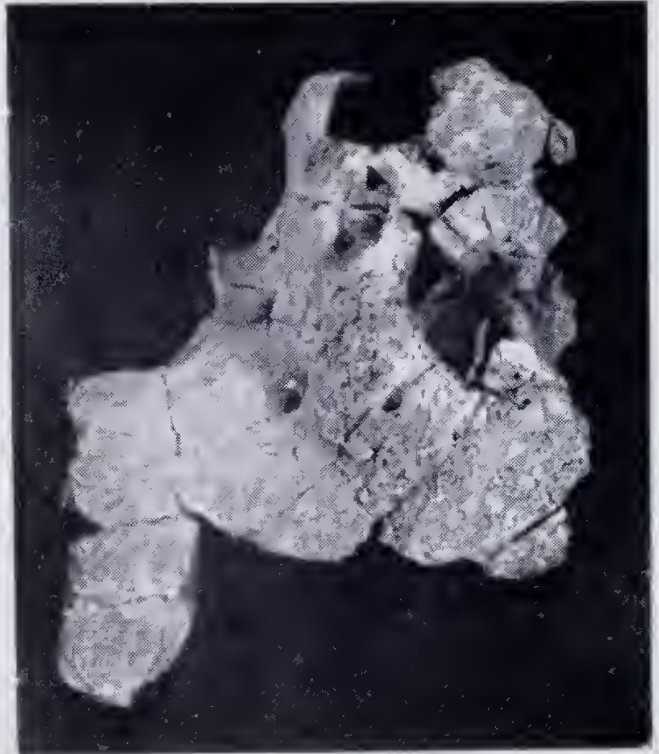
Scutes.—A fragmentary dorsal scute (CPC 17113); several fragmentary ventral scutes (CPC 17114).

Although all the scutes are very fragmentary it proved possible to reconstruct one dorsal and several ventral plates. Three features can be compared with known characters of other crocodilian scutes (Table 2). The dorsal scute (CPC 17113) can be distinguished from those of the Crocodylinae (except *Crocodylus johnsoni*, Fig. 3B), *Alligator* and the Gavials by the possession of an anterior bevelled margin which is overlapped by the smooth under surface of the

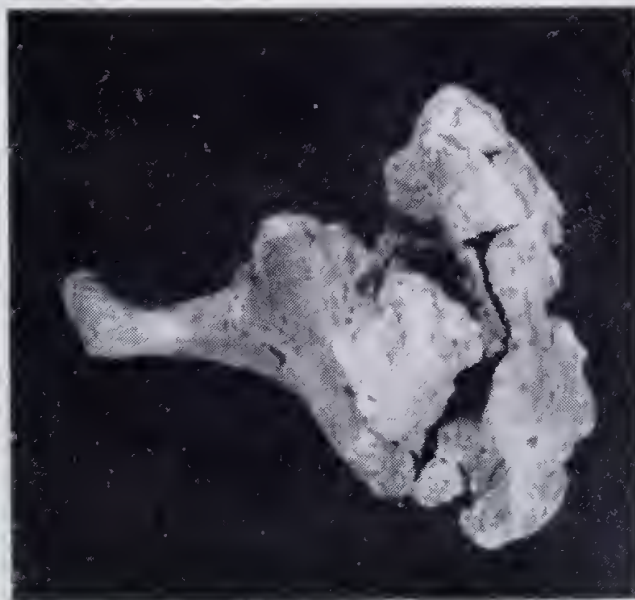
preceding scute. The Windjana scutes may be distinguished from Alligatorinac scutes which are each composed of two parts united longitudinally by a suture (Kalin 1955). The possession of a longitudinal ridge on the dorsal scutes is characteristic of most crocodilians (Table 2) except *Alligator*, and this ridge is also lacking in the Windjana specimen. The Windjana specimen has serrated transverse sutures, a condition which rarely occurs in



A



B



C



D

Figure 2.—A.—Dorsal view of left premaxillary fragment (CPC 17112), of *Crocodylus* sp. indet. from Windjana Gorge. x0.75. B.—Ventral view of same x0.75. C.—Frontal view of same x0.75. D.—Ventral view of left palate of *Crocodylus porosus* from the Northern Territory (Specimen courtesy of R. Jenkins). x0.75.

Alligator, *Crocodylinae* and *Gavials*, in which the scutes lie free in the integument (Kalin 1955). The possession of lateral sutures by the Windjana specimens ranks the fossil form with *Jacare*, *Caiman*, *Pallimnarchus* and *Crocodylus johnsoni* (a longirostrine form) and the Chinchilla specimens.

There is only slight angulation apparent on the dorsal scute, similar in degree of curvature to that on dorsal scutes of *C. johnsoni* examined,

which serves to distinguish the scute from *Jacare*, *Caiman*, *Pallimnarchus* and the Chinchilla scutes.

Flat scutes (CPC 17114), similar in shape to scutes designated ventral by de Vis (1885), are present in the Windjana collection. These scutes, here identified as ventral scutes, do not possess crests or angulations, and also have an anterior bevelled edge and transversely serrated sutures, as in the Chinchilla scutes examined.

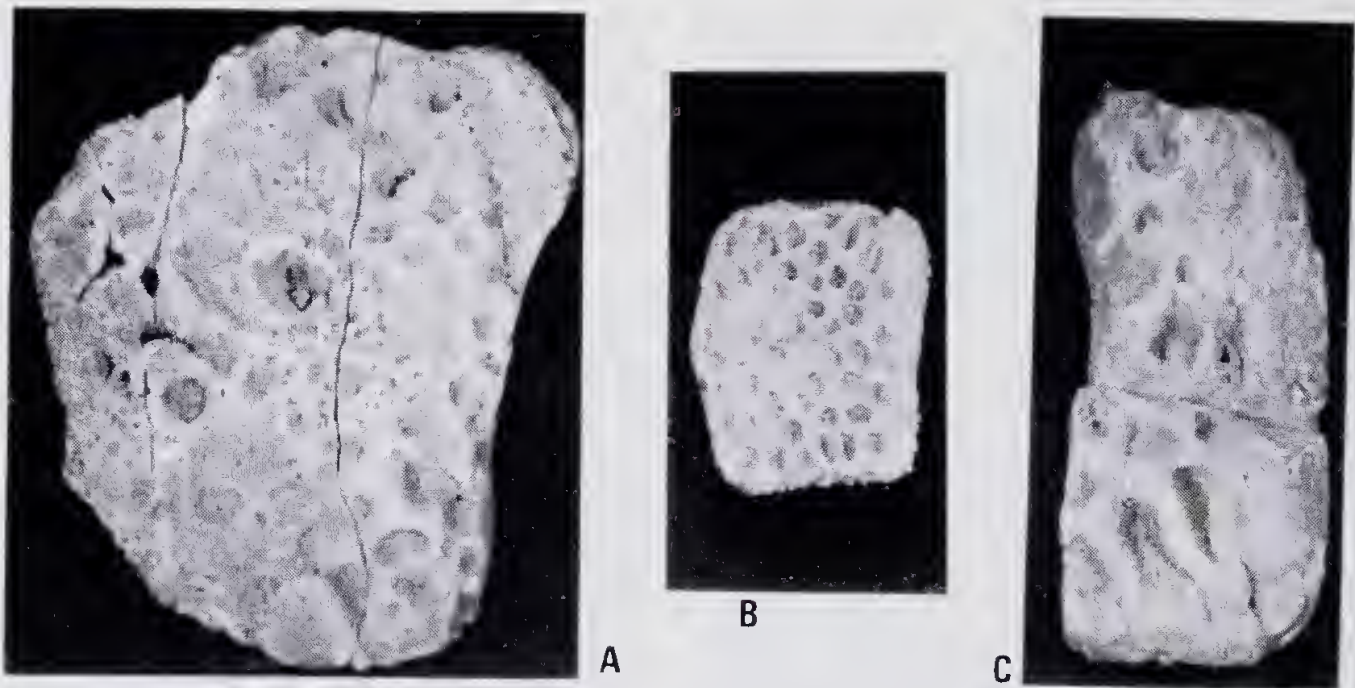


Figure 3.—A.—Dorsal scute of *Crocodylus* sp. indet. from Windjana Gorge (CPC 17113). x 1.0. B.—Dorsal scute of *Crocodylus johnsoni* from Windjana Gorge (CPC 17115). x 1.0. C.—Ventral scute of *Crocodylus* sp. indet. from Windjana Gorge (CPC 17114). x 1.0.

Table 1
Characteristics of crocodilian premaxillary and teeth morphology

	Number of premaxillary teeth	Pseudoheterodont	Medial mandibular occlusion	Notch	Tooth morphology	Ornament of teeth
Windjana premaxillary	25 (4)	Yes	Yes	Yes	Rounded ?
Chinchilla premaxillary	+6	Yes	Yes	Sub-rounded ?
<i>C. porosus</i>	4 (3)	Yes	No	Yes	Sub-rounded	Smooth
<i>C. acutus</i>	5 (4)	Yes	No	Shallow	Sub-rounded	..
<i>C. vulgaris</i>	5 (4)	Yes	No	Yes	Sub-rounded
<i>C. johnsoni</i>	5 (4)	Slight	No	Shallow	Sub-rounded
<i>P. pollens</i> (de Vis, 1885)	5 (4)	Yes	?	Yes	Cylindrical, prominent anterior and posterior carinae
<i>P. pollens</i> (Longman, 1925b)	5 (4)	Yes	?	Yes	" "	Minutely rugose on carinae
<i>P. sp</i> teeth (W. Australia)	"	" "	" "
Alligatorinae	5 (4)	Yes	Yes	No
Gavials	5	No, but 1st pm tooth strongest	No	No	Slightly curved and pointed

Data from: Huxley (1859), Kalin (1955), de Vis (1885), Longman (1925a), Longman (1925b), Iordansky (1973) and personal observations. Figures in brackets indicate number of largest premaxillary tooth.

Table 2
Characteristics of crocodilian scutes

	Lateral edges united by sutures	Anterior edge bevelled	Longitudinal ridge present	Angulation	Ventral scutes
<i>Jacare</i>	Yes	Yes	Yes	Yes	Yes
<i>Caiman</i>	Yes	Yes	Yes	Yes	Yes
<i>Alligator</i>	Rarely	No	No	No	No
Crocodylinae	Rarely	No	Yes	No	No
<i>Crocodylus johnsoni</i>	Yes	Yes	Yes	Yes	No
Gavials	Rarely	No	?	No	No
Chinchilla scutes	Yes	Yes	Yes	Yes	Yes
<i>Pallimnarchus</i> sp.	Yes	Yes	Yes	Yes	Yes
Windjana scutes	Yes	Yes	No*	No*	Yes

* Only one dorsal scute in collection (CPC 17113).

Data from Huxley (1859), Kalin (1955), Longman (1925 a & b), de Vis (1885) and personal observation.

The possession of ventral scutes serves to distinguish the Windjana crocodilian from the Crocodylinae, *Crocodylus johnsoni*, *Alligator* and Gavials (Huxley 1859).

Thus on scute morphology alone, the Windjana crocodilian is distinct from the Crocodylinae and Gavials and seems to have more in common with the Alligatorinae (excluding *Alligator*) but to be distinct also from *Jacare*, *Caiman*, *Pallimnarchus* and the Chinchilla form. In the absence of more material it is impossible to place the affinities of the Windjana form more closely with any of the described crocodilians. An attempted diagnosis of the species is presented below.

Diagnosis: A brevirostrine form, with 5 premaxillary teeth, pseudoheterodont, a premaxillary-maxillary notch, mandibular teeth occluding inside the upper series, dorsal and ventral scutes, scutes without crests or angulations but having an anterior bevelled edge and laterally sutured edges.

The Windjana crocodile was a large animal. The recent specimen of *C. porosus* examined had a body length of just over 5 m (R. Jenkins, pers. comm.). By comparison of the size of the premaxillary of the *C. porosus* specimen and our Windjana fossil we estimate the length of our animal to have been about 7 m.

Order Chelonia

Suborder Cryptodira

Superfamily Carettochelyoidae

Family Carettochelyidae

Genus *Carettochelys* Ramsay

Carettochelys sp.

(Fig. 4C.)

Material studied.—Fragmentary plastron with ridged ornamentation (CPC 17118).

Carettochelyid turtles, characterised by *Carettochelys insculpta*, are at present found only in New Guinea and the extreme north of the Northern Territory (Cogger 1975). According to Ogilby (1905, p. 28, 29) the carapace and plastron plates are covered with "small, round, raised rugations or wavy irregular raised lines between shallow sculptures". The only other turtles having a similar ornament are the Trionychids, represented in Australia by *Trionyx australiensis* described from Queensland (de Vis 1894). Gaffney recently re-examined the remains and corroborated the original interpre-

tation (Gaffney 1976). The ornament is described as "irregular longitudinal ridges associated with generally weaker, less regular, transverse ridges giving pocketed appearance" (Hill *et al.* 1970, pl. Cz VII, fig. 8). The original drawing figured by de Vis (1894, pl. X) indicates that in *Trionyx* the ridges are thinner than the broadly sculpted intervening "valleys". This situation in *Trionyx* is the opposite of that displayed by the Windjana fossil (Fig. 4C), in which the ridges are broad and rounded and surrounded by intervening narrowly incised grooves, similar to the pattern described for *Carettochelys* by Ogilby (1905).

On the figured specimen, a pustular pattern is developed, suggesting that the fragment came from a more central part of the plate; towards the lower plate borders the ridges take on an elongated form parallel to the sutures (Ogilby 1905). The pattern on the specimen compares closely with that illustrated by Glaessner (1942, pl. X) of *Carettochelys* from Miocene deposits of New Guinea. Glaessner (1942, p. 107) described the ornament as "*Trionyx*-like granulation consisting of isolated small rounded or elliptical mounds separated by narrower or equally wide anastomosing depressions".

This distinctive ornamentation alone is sufficient to place some of the Windjana chelonians in the genus *Carettochelys*.

Suborder Pleurodira

Family Chelyidae

Genus ?*Chelodina* Fitzinger

?*Chelodina* sp.

(Figs. 4A, B, F, G.)

Material studied.—Plastron fragments and unidentifiable bones, including a broken and water-worn right first pleural plate (CPC 17117), and a ?second left pleural plate, only the medial part of which is preserved (CPC 17116).

Comparison was made with known fossil and recent chelonians described in the literature and plates were orientated by reference to a carapace of recent *Chelodina longicollis* in the Bureau of Mineral Resources Palaeontological Museum.

First pleural plate.—The largest pleurodire fragment present in the collection (Fig. 4F) is an anterior right pleural plate (CPC 17117) which is both incomplete and waterworn. No surfical ornament is present, the posterior lateral mar-

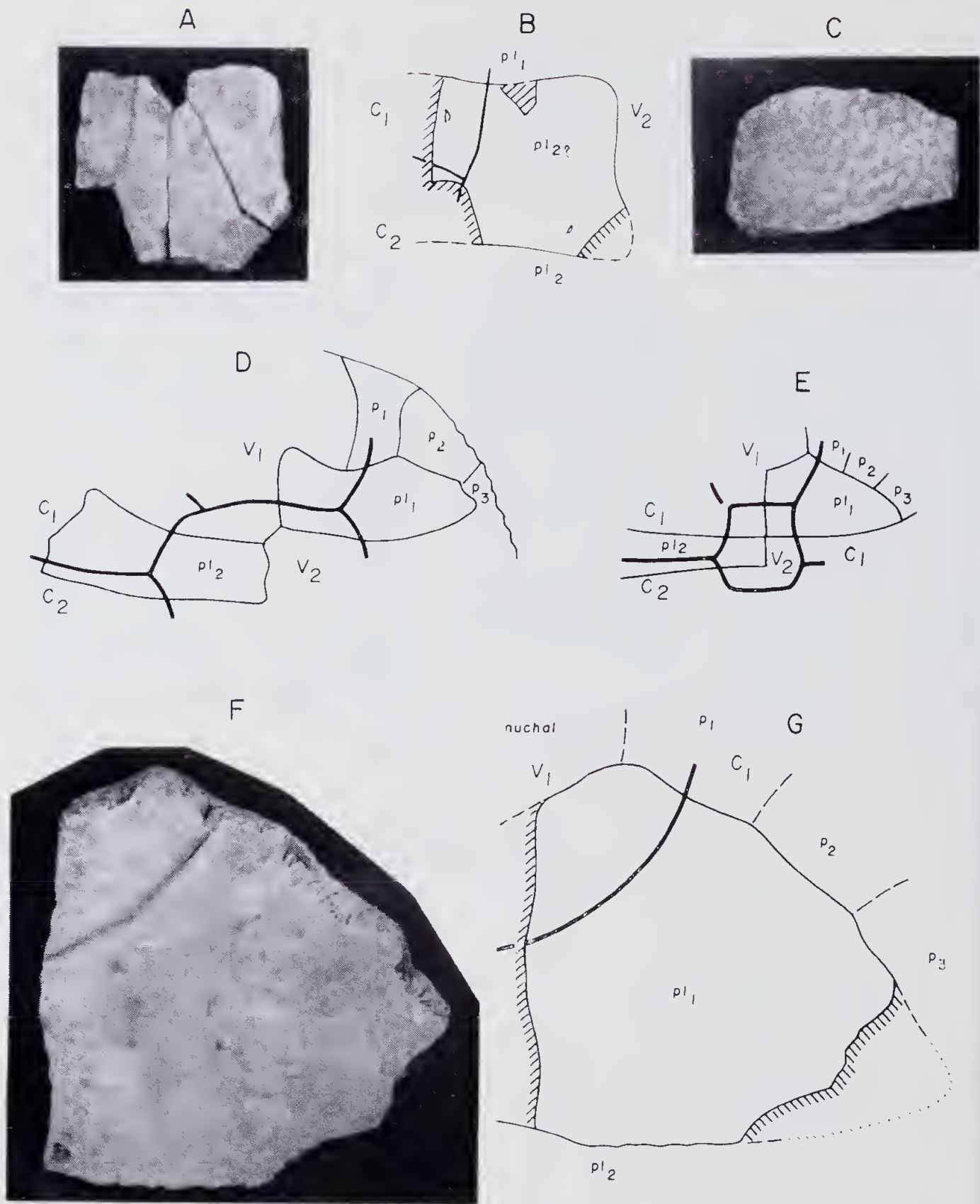


Figure 4.—A.—Dorsal view of ?left second pleural plate (CPC 17116) cf. ?*Chelodina* sp. from Windjana Gorge. x1.0. B.—Sketch of same. C.—Fragmentary plate of *Carettochelys* sp. (CPC 17118) from Windjana Gorge. x1.0. D.—Sketch of anterior dorsal carapace of *Emydura* sp. aff. *E. macquari* (after Warren 1969). E.—Sketch of anterior dorsal carapace of *Chelodina longicollis* (after Cogger 1975). F.—Right fragmentary first pleural plate (CPC 17117) of ?*Chelodina* sp. from Windjana Gorge. Dorsal view. x1.0. G.—Sketch of same. Key: Heavy lines—trace of shield; fine lines—plate boundaries: pl₁—first pleural plate; pl₂—second pleural plate; p₁₋₃—peripheral plates; n—nuchal plates; V₁—first ventral shield; V₂—second ventral shield; C₁₋₂—first and second costal shields; diagonal shading—fracture.

join is broken, and the medial portion of the plate is absent. The sutures for connection to the nuchal and three peripheral plates are present as is a partial suture with the second right pleural plate. In the anterior medial portion of the plate the trace of the join between the first vertebral shield and the first costal shield is present. This line rises on the border of the first pleural plate, probably about midway along the contact with the first peripheral plate, and swings posteromedially across the plate (Fig. 4G). In *Chelodina longicollis* the triple junction formed by the meeting of the first pleural, first peripheral, and nuchal plates is anterior to this line (Fig. 4E) and the first plate forms a triangular shaped, forward oriented projection at this junction. In *Emydura* sp. aff. *E. macquari* (figured by Warren 1969) this triangular projection occurs at the join of the first and second peripheral plates and behind the first vertebral shield trace (Fig. 4D). The lateral margin of the fossil first pleural plate has a scalloped appearance and suggests that three peripheral plates adjoined it and in reconstruction (Fig. 4G) the trace of the first vertebral shield would cross onto the first peripheral behind the triple junction formed on the first pleural, first peripheral, and nuchal plates. Hence the affinities of the fossil are probably closer to *Chelodina* than *Emydura*. Comparison of the fossil plate with the recent specimen of *Chelonia* figured by Cogger (1975) excludes our specimen from that genus also.

The angle of the triangular projection, measured along a vector of the nuchal suture and a vector from the triple point junction to the join of the second and third peripherals at the lateral margin of the first pleural plate, is 120° on the recent specimen of *Chelonia longicollis* examined and approximately 35° on the fossil specimen. Comparison with other Australian forms such as *Pseudemydura*, *Elseya*, or the fossil horned turtle *Meiolania* were not made. In the absence of such comparisons the fossil is tentatively assigned to ?*Chelonia* sp.

Second pleural plate.—A fragmentary ?second left pleural plate (CPC 17116) is present in the collection (Fig. 4A). The medial suture is almost complete, but as only the medial part of the plate is present the sutures with the first and third pleural plates are only partly preserved. The trace of the junctions between the first and second costal shields and the second vertebral shields is present (Fig. 4B). The angle formed at the triple junction of these shields is more acute towards the anterior of the fossil and compares (Fig. 4B) more closely with this feature on *Chelodina longicollis* examined than with *Emydura* sp. aff. *E. macquari* figured by Warren (1969). However, as the variability of the shield traces is unknown to the authors, it is only tentatively accepted that this feature suggests affinities of the fossil with *Chelodina* sp.

Reptilian fossils from Jubilee Dam

We have examined fragmentary bone collected by K. McKenzie in 1960 from Jubilee Dam, about 11.2 km north of Quanban Homestead in

the Kimberley area (Merrill 1968) and now lodged in the Western Australian Museum. The fossils, all numbered 60.10.10 consist of fragmentary crocodilian scutes, recognised by their characteristic ornamentation, one peg-like tooth, probably crocodilian and five waterworn pieces of bone. While one fragment has the characteristic cross-hatched pattern of the inner side of crocodilian scutes, other pieces are very similar in bone morphology to our ?*Chelodina* fragments from Windjana Gorge. It is thus suggested that at least some of the fossil material collected by McKenzie is chelonian.

Depositional environment

The cave that contains the bone conglomerate was probably formed at river level. Similar karst features are now forming at river level in Windjana Gorge (Lennard River) and the nearby Geikie Gorge (Fitzroy River).

Deposition of gravel in the cave may have been roughly contemporaneous with cave formation or could have taken place at some later time during river flooding. The present-day Lennard River is depositing gravel only in the bed of the main channel and not on the banks. If we assume a similar flow regime at the time of deposition of the conglomerate, then the cave must have been at or near the level of the river bed, and the conglomerate represents the former level of the river bed.

The bone material is fragmentary, but much of this fragmentation appears to have occurred during weathering from the outcrop. Most of the bone fragments do not appear to be markedly abraded or waterworn, but partial skeletal disarticulation probably took place prior to deposition as there are no articulated bones present.

The remains of crocodiles and turtles in this deposit do not have any important palaeo-environmental significance as both suborders occur in the nearby area. However, this new discovery would represent a significant range extension of *Carettochelys*.

The presence of the river turtle *Carettochelys*, at present commonly only in New Guinea, may imply a warmer climate in north-western Australia during the past, but without more evidence these conclusions are speculative. The amount of down-cutting of the Lennard River suggests that the river once carried appreciably more water at some time in the past, a conclusion consistent with the presence of the large crocodilian.

Age of the fossil deposit

Tertiary and Quaternary deposits are poorly known in the Kimberley area. Guppy *et al.* (1958, p. 63) gave the name Warrimbah Conglomerate to unconsolidated coarse gravels found 50 to 130 km downstream from Geikie Gorge in the Fitzroy River, about 25 m above the present flood plain (Jennings & Sweeting 1963, p. 13). Veevers & Wells (1961) have suggested correlation of the Warrimbah Conglomerate with high-level gravels at Windjana Gorge, from which a diprotodontid femur, collected by Hard-

man (1884), was thought to be derived. They suggested a Pleistocene age for both the Warrimbah Conglomerate and the high level gravels at Windjana Gorge.

The topographic height of the high level gravels at Windjana Gorge is not known but it is probable that the Lennard River has dissected several levels marking former land surfaces. As the reptile fossil site occurs in sediments 41 m above the river bed, it does suggest that these sediments would be among the oldest of any series of fluvial deposit. Hence correlation with the Warrimbah Conglomerate gives a minimum age of Late Pleistocene for the fossils.

The presence of reworked laterite pebbles in the deposit suggests a post-laterite age. Lateritization in the Perth Basin has been dated as Late Oligocene to Early Miocene by Schmidt and Embleton (1976), although Playford *et al.* (1975) believe that most laterite in the basin is of Pleistocene age. Furthermore Playford *et al.* (1975) point out that whilst the period of lateritization in the Canning Basin is generally regarded as Tertiary, an Early Pleistocene age cannot be discounted. If Schmidt and Embleton are correct, and if lateritization was contemporaneous over the whole State, then the fossil site may be as old as Early Miocene.

On the basis of the fossils collected from Windjana Gorge no precise age can be affixed to the site and the conglomerate is too coarse and well oxidized to retain pollen. No mammalian remains were recovered from the site and it is therefore impossible to correlate the conglomerate with dated vertebrate sites elsewhere in Australia. However, some general comments can be made. *Carettochelys* is known from Miocene deposits in New Guinea (Glaessner 1942) and *Chelodina* ranges from ?Oligocene to Recent (Romer 1966). As the reference for the ?Oligocene age is not cited by Romer it is not possible to comment on the validity of this date. Accordingly, we have assigned the age of the Windjana fossil site as probably late Cainozoic.

Conclusions

Although the remains are very fragmentary, three distinct groups are recognized. These include an indeterminate crocodilian, a river turtle (*Carettochelys* sp.) and a pleurodire turtle questionably assigned to the genus *Chelodina*.

The presence of these fossils in the Windjana Gorge area may be evidence for a more humid climate during the late Cainozoic than the semi-arid one of today.

Acknowledgements.—We would like to express our thanks to R. Jenkins for providing the specimen of *Crocodylus porosus*, M. Archer of the Queensland Museum for the Chinchilla material, D. Merrilees of the Western Australian Museum for advice and Western Australian specimens and P. E. Playford for information on the elevation of the fossil site. The photographs were taken by R. W. Brown of the Bureau of Mineral Resources. All specimens are deposited in the Commonwealth Palaeontological Collection (CPC) at the Bureau of Mineral Resources, Canberra. This paper is published with the permission of the Director, Bureau of Mineral Resources.

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Chromosome numbers in Western Australian Plants, I.

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Manuscript received 22 March 1977; accepted 21 June 1977

Abstract

Chromosome numbers for 33 species are given. The counts on *Acanthocarpus* ($n=16$), *Billardiera* ($n=12$), *Macgregoria* ($n=10$), *Muiriantha* ($n=14$), *Sollya* ($n=12$) and *Tricoryne* ($n=28$) are first records for these genera.

Introduction

The flora of Western Australia is poorly known in most aspects of its biology and classification. Chromosome numbers are available for less than 5% of the species of angiosperms occurring in the region, and the majority of such counts are from a single locality. The aim of this series is to add to the number of available counts, especially in neglected groups. This report deals with species collected from a number of widely scattered localities, including a series collected in the North West Cape region during 1976.

Materials and methods

Buds were fixed in Bradley's (1948) fixative, stained in Snow's (1963) acid-alcoholic carmine for 4-7 days, then squashed in 45% acetic acid to observe pollen mother cell meiosis. Slides were made permanent by removing the coverslip in absolute alcohol and remounting in euperal. At least 5 cells were counted before the count was accepted.

Results

Chromosome numbers, details of collection localities and vouchers are given in Tables 1 and 2. Vouchers are deposited in K.P. (King's Park) and PERTH.

Discussion

Table 1.—Turner (1966) reported $n=9$, 10, 15 and 16 for five species of *Stackhousia*, the only other genus of the family Stackhousiaceae. Until further cytological and taxonomical work is undertaken on this genus, possible relationships between the monotypic *Macgregoria* ($n=10$) and the species of *Stackhousia* which are $n=10$ (*S. huegelii* and *S. aff. georgei*) cannot be ascertained.

The count on the *Logania* sp ($n=8$) is the first diploid count for the genus, the only previous count was $n=16$ for *L. flaviflora* by Keighery (1975). This suggests that $n=8$ is the basic number for the genus.

The finding of $n=14$ for the monotypic *Muiriantha* reflects its close relationship to *Chorilaena* ($n=14$) and its placement in the Sub-tribe Nematolepidinae (Smith-White, 1954) is further substantiated.

Almost nothing has been published on the cytology of Australian Pittosporaceae, so it is difficult to comment on the new records for *Sollya* ($n=12$) and *Billardiera* ($n=12$).

Table 2.—Sands (1975) in her study of the cytoevolution of the Australian Fabaceae found polyploidy to be rare (14 of 242 species examined) and concluded it to be of little significance for the tribe Podalyrieae (the major group of Australian peas). However, the tribe Cotuleae (the arid zone peas) including *Swainsonia* contains only polyploid species. This suggests that polyploidy may not have been of major evolutionary significance to woody temperate species, but is probably of major significance to Eremean herbaceous species.

The two counts recorded for the genus *Tephrosia*, $n=8$ for *T. purpurea* by Sands (1975) and $n=11$ for *T. flamea* are strikingly different. Further studies are needed on this genus.

All counts recorded for the three species of Liliaceae are at the tetraploid level. Related taxa in southern Western Australia show $n=8$ (*Acanthocarpus*) and $n=14$ (*Tricoryne*) (Keighery, unpub. data).

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Table 1
Miscellaneous species

Taxon	N	Locality	Voucher ¹
Proteaceae			
<i>Adenanthos detmoldii</i> F.Muell.	13	Scott River	GK. 599
<i>Franklandia fucifolia</i> R.Br.	14	30 km W. Israelite Bay	GK. 220
<i>Personia aricularis</i> F.Muell.	7	6 km N. Cockleshell Gully	GK. 588
<i>P. aff. comata</i>	7	20 km E. Jurien Bay	GK. 576
<i>P. saccata</i> R.Br.	7	King's Park	F. 109
Stackhousiaceae			
<i>Macgregoria racemigra</i> F.Muell.	10	85 km N. Mt. Newman	D. 4397
Loganiaceae			
<i>Logania</i> sp.	8	16 km E. Mt. Hampton	GK. 36
Pittosporaceae			
<i>Billardiera coriacea</i> Benth.	12	8 km S. Ongerup	GK. 159
<i>Sollya heterophylla</i> Lindl.	12	Albany	GK. 169
Rutaceae			
<i>Muiriautha hassellii</i> C.A.Gard.	14	Stirling View Pass Road	GK. 186
<i>Philothea tubiflora</i> A.S. George	14	50 km N.E. Laverton	GK. 522
Fabaceae			
<i>Daviesia acanthocolona</i> F.Muell.	9	142 km E. Kalgoorlie	GK. 535
<i>Kennedia prorepens</i> F.Muell.	11	60 km W. Neale Junction	GK. 567
Goodeniaceae			
<i>Velleia connata</i> F.Muell.	8	60 km S. Neale Junction	GK. 553
Brunoniaceae			
<i>Brunonia australis</i> R.Br.	9	60 km S. Neale Junction	GK. 547
Asteraceae			
<i>Podolepis capillaris</i> (Steetz) Diels	3	Pioneer Rock S. of Balladonia	GK. 192
<i>Cotula coronopifolia</i> L.	10	Old Chittering Townsite	GK. 55

¹GK—author, D—Demarz, F—Fairall.

Table 2
Northern species

Taxon	N	Locality	Voucher ¹
Fabaceae			
<i>Alysicia cinerea</i> (F.Muell.) Benth.	11	20 km N. Nanutarra	GK. 793
<i>Brachysema aphyllum</i> Hook. (erect form)	8	5 km S. Paynes Find	GK. 798
<i>Brachysema macrocarpum</i> Benth.	16	72 km N. Minilya to Exmouth	GK. 812
<i>B. macrocarpum</i>	16	8 km S. Vlaming Head	GK. 823
<i>Isotropis atropurpurea</i> F.Muell.	6	12 km S. Bullara	GK. 827
<i>Jacksonia</i> sp.	9	5 km S. Paynes Find	W. 1779
<i>Lotus cruentus</i> Court	14	39 km S. Learmonth	GK. 820
<i>Psoralea</i> sp.	11	53 km S. Learmonth	GK. 819
<i>Swainsonia kingii</i> F.Muell.	16	4 km S. Vlaming Head	GK. 822
<i>Swainsonia occidentalis</i> F.Muell.	16	50 km N. Minilya to Exmouth	GK. 802
<i>Tephrosia flamea</i> (F.Muell.) Benth.	11	2 km S. Binthalya	W. 1795
<i>Templetonia egna</i> (F.Muell.) Benth.	8	202 km S. Cobra Station Homestead	W. 1750
Brassicaceae			
<i>Stenopetalum robustum</i> Endl. var. <i>pedicillare</i> (F.Muell.) Shaw	5	50 km N. Minilya to Exmouth	GK. 801
Asteraceae			
<i>Brachycome iberidifolia</i> Benth.	9	50 km N. Minilya to Exmouth	GK. 803
Liliaceae			
<i>Acanthocarpus</i> sp.	16	Coral Bay Turnoff	GK. 816
<i>Tricoryne</i> sp.	28	72 km N. Minilya to Exmouth	GK. 814

¹GK—author, W—Wittwer.

Some Eocene leaf fragments comparable to Proteaceae.

by R. T. Lange

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(communicated by B. E. Balme)

Manuscript received 20 September 1977; accepted 25 October 1977

Abstract

Six hundred Eocene leaf fragments from Australian deposits were compared with four thousand small fragments arbitrarily drawn from Australian region perennial angiosperms, to examine similarities between Eocene and living forms. Various instances of similarity were detected and those involving Proteaceae were examined in detail. Four fossils are described. One from Western Australia resembles *Synaphea* and the others, from South Australia, include evidence for *Darlingia*. The evaluation of their evidence and the ascription of the fossils to living taxa are discussed in relation to the circumspection evident about both issues in Australian literature.

Introduction

In Australian Tertiary deposits there are many strata that contain carbonaceous fossil angiosperm leaves. Where they outcrop or are exposed by quarrying the long-established study of whole-leaf and shoot compressions may proceed, but for every leaf-bearing stratum that outcrops in South Australia for example, perhaps a hundred others are known only from drill cores which yield only fragments not whole leaves. The question arises as to what palaeontological evaluations can be made of the evidence presented by such fragments.

Three viewpoints seem relevant. First, the fragments can be scanned for fossil epiphyllous microfungi (Felix 1894, Edwards 1923, Cookson 1947, Dilcher 1965, Lange 1969, 1976, Selkirk 1972, 1975). In this regard fragments are little less informative than whole leaves, and so have the advantage of permitting access to epiphyllous microflora in drill-core samples.

Second, the fragments have been studied with a view to developing catalogues and classifications of their variety, without reference to the taxonomy of living angiosperms, to assist correlation (Arbeitsgruppe Cuticulae 1964, Meyen 1966, Lange 1969b). Little progress with this approach is evident in Australia.

A third possible viewpoint is that the fragments might be amenable in some degree to the same approach used on whole-leaf compressions, i.e.—to arguments that their source plants were or might have been relatives of particular living angiosperm taxa. This is a difficult viewpoint to maintain. First, it appeals to similarity between living and fossil leaves as demonstration that they are of the one stock whereas ancestral leaves must involve dissimilarities with descendants. Further, ascription of fossils to living taxa is justified scientifically only when it contributes to rigorous accounts of their prehistory, evolution and phylogeny but evidence is that the fossil angiosperm literature has a poor Australian acceptance in that regard. Thus a substantial literature about fossil *Eucalyptus* is ignored by

Johnson (1972) and is described by Carr and Carr (1969) as "... utterly inadequate." while that dealing with fossil Proteaceae is criticized for its erroneous claims (Johnson and Briggs 1963) and is described as "... the absence of a useful fossil record" (Johnson and Briggs 1975). There is no reason to believe that deductions based on leaf-fragments will be better received.

On the other hand no Australian investigation seems to have been reported on the potentials and limitations of the approach as it applies to dispersed Tertiary leaf fragments, and to dismiss it out of hand is to risk ignoring substantial evidence about the prehistory of some taxa, perhaps the only fossil evidence. The present study therefore takes up the question on the basis of crossmatching between 600 Eocene fossil fragments and 4 000 fragments representing a wide range of living perennial angiosperms from the Australian region.

For the great majority of the fossils, no matches of a provocative, exclusive nature were detected. In a small minority of cases, fossils resembled the representatives of a particular living taxon in the 4 000-fragment sample and were dissimilar to all the others. Cases involving Proteaceae were selected for an evaluation which is reported here.

First a detailed acquaintance with leaf cuticles of Proteaceae was gained from a specially assembled slide collection, then the fossil leaf fragments were individually examined for close similarity with living Proteaceae. Four of the matches are described and discussed with regard to the evidence they provide. The issue of their ascription to Proteaceae is then considered.

Materials and methods

The source sediments of the fossils described were carbonaceous clays from Lake Lefroy, Western Australia (University of Western Australia Geology Department sample 76768 Lake Lefroy WMC KD 3009A 50m) supplied by D. Hos of the South Australian Mines Department,

who determined its palynological age as late Eocene, and from Maslin Bay, South Australia (Lange 1970), determined as early Middle Eocene by McGowran, Harris and Lindsay (1970). Others from which fragments were recovered were from Golden Grove, South Australia and Anglesea Power Station, Victoria, both considered on the basis of unpublished palynological studies to be of Eocene age (W. Harris, pers. comm., Dec. 1976).

Samples digested in Schultz solution yielded small chips of leaf from which the cuticles, freed by dilute KOH solution, were mounted unstained in phenol glycerine jelly. Cuticles from living plants were prepared similarly (Lange 1976). Phase contrast and Nomarski interference phase contrast microscopy were used to study them. Because the coloured images of Nomarski observation yield poor monochrome photographs, the latter were supplemented with drawings. To extend comparisons with Proteaceae, cuticle slides were prepared from herbarium specimens including many kindly supplied by Dr. L. A. Johnson of the National Herbarium of New South Wales who with Dr. Briggs has provided the major account of the evolution and classification of the family (Johnson and Briggs 1975). This included slides from Proteaceae ascribed to *Adenanthos*, *Agastachys*, *Banksia*, *Bellendena*, *Buckinghamia*, *Cardwellia*, *Cenarrhenes*, *Champeria*, *Conospermum*, *Darlingia*, *Diastella*, *Dryandra*, *Embothrium*, *Fauria*, *Finschia*, *Franklandia*, *Grevillea*, *Hakea*, *Helicia*, *Hicksbeachia*, *Isopogon*, *Kermadecia*, *Knightia*, *Lambertia*, *Leucospermum*, *Lomatia*, *Macadamia*, *Oreocallis*, *Orites*, *Petrophile*, *Persoonia*, *Protea*, *Roupala*, *Serruria*, *Stenocarpus*, *Stirlingia*, *Strangea*, *Symphionema*, *Synaphca*, *Telopea* and *Xylomelum*.

Descriptions of the fossils

Lake Lefroy cf. Proteaceae I

Slide Lake Lefroy cf. Proteaceae I, Adelaide University Botany Department, see Figs. 1-16. The fragment consisted of a 5 mm length embracing a central straight rib with torn lateral fringes of blade and was bifacial with dissimilar surfaces. The cuticle of the stomatiferous surface is thin and fragile relative to that of the non-stomatiferous which is thick and robust. Outlines express venation on both cuticles, pronounced on the stomatiferous where it is associated with contrasting cell outlines and subdued on the reverse where one type of cell extends over veins and between them.

Figure 1 is a zone-diagram of the stomatiferous cuticle. Lateral veins about 80 μm wide leave the main vein at right angles at intervals of about four times their breadth and are approximately opposite. Central cell outlines of the main vein (zone A) are straight, narrow, about 5 x 55 μm in most cases and strictly parallel along the rib. Infrequent small cells bear a stubby papilla up to 25 μm long. Each is cylindrical truncate and rounded off not torn at the summit (Figs. 5, 14). The trend of cell long axis along the rib is less strict at its margins (zone B, Figs. 3, 11). Outlines are relatively

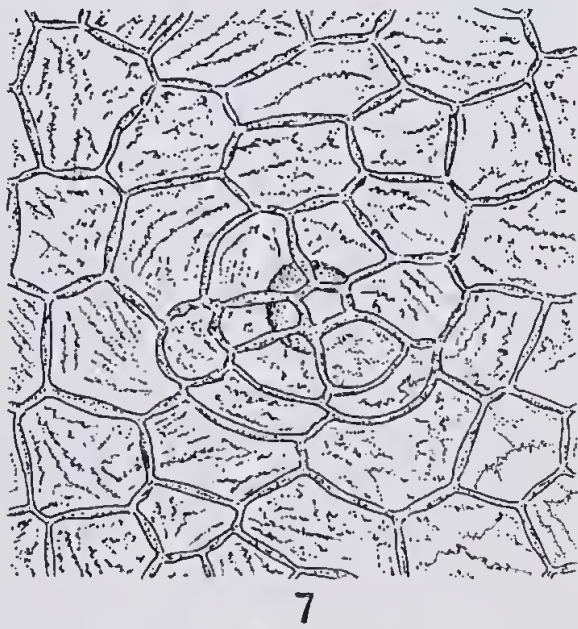
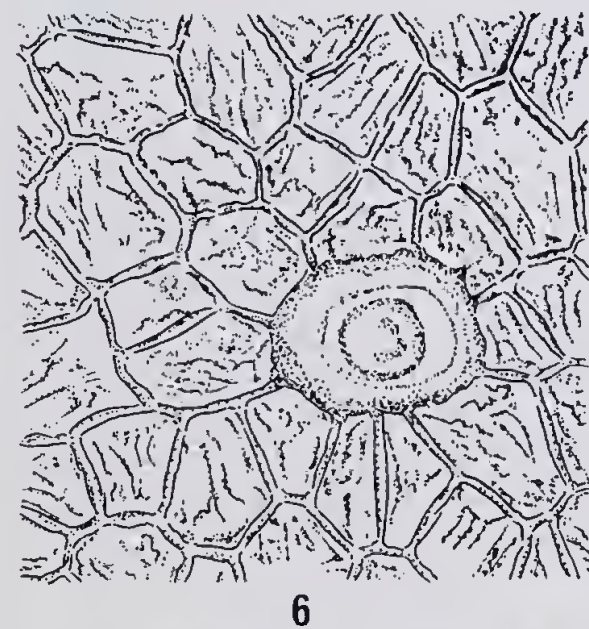
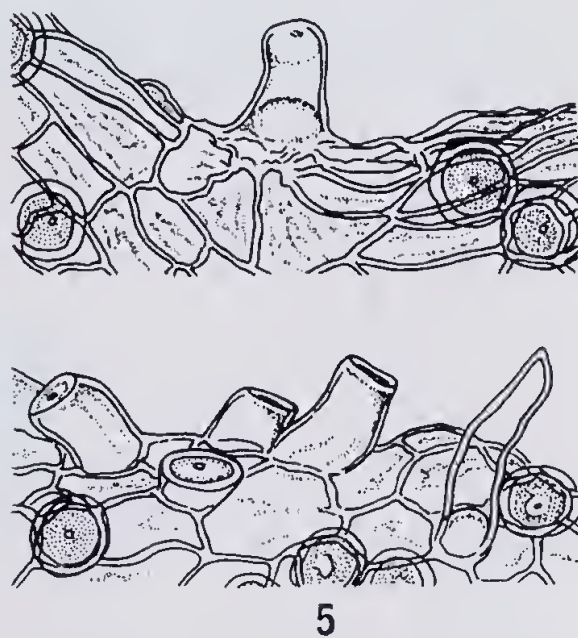
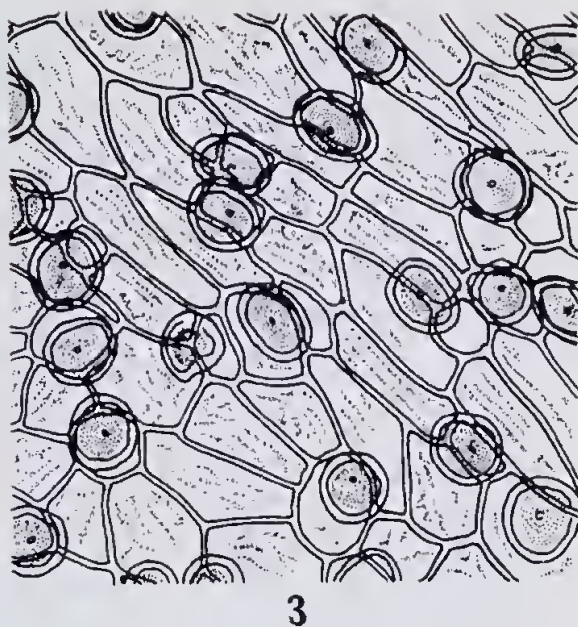
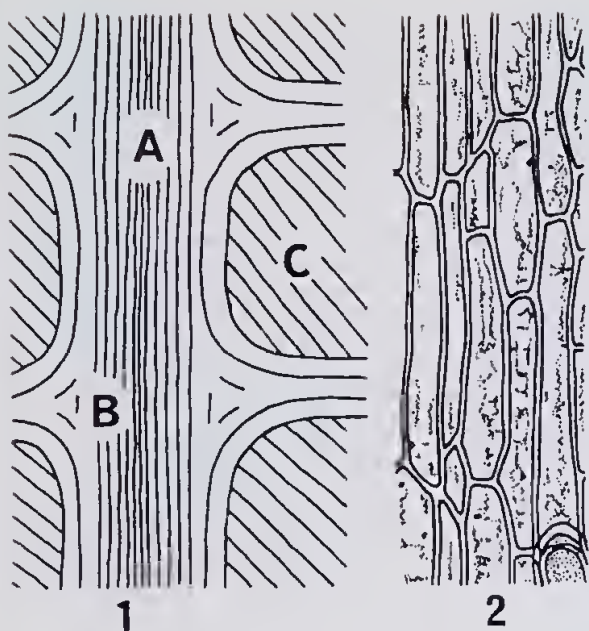
broader and shorter and some are compact polygonal. There are more small outlines with the papilla, about 1500-2000/mm² of leaf surface. In the transition between main and lateral venation the trends of cell long axis orientation are as shown in the zone diagram.

Cuticle of the leaf blade between lateral veins (zone C) contrasts with the rest. Cell wall traces are fainter, are compact polygonal and have no trend of orientation (Figs. 4, 12, 13). Most of the smaller cells bear the same papilla as in zone B but some carry a simple, unicellular hairshaft 40-50 μm long (Figs. 4, 5, 14, 16). It may be curved or nearly straight, has thick unornamented walls and is acute (Fig. 16). Scattered in zone C are stomatal traces which are difficult to see and relatively sparse. Each consists of a thin, translucent area of cuticle with a delicate narrow elliptical slit-like trace about 3 x 12 μm in its centre (Figs. 4, 12, 13). They have no particular orientation, and appear to be anomocytic.

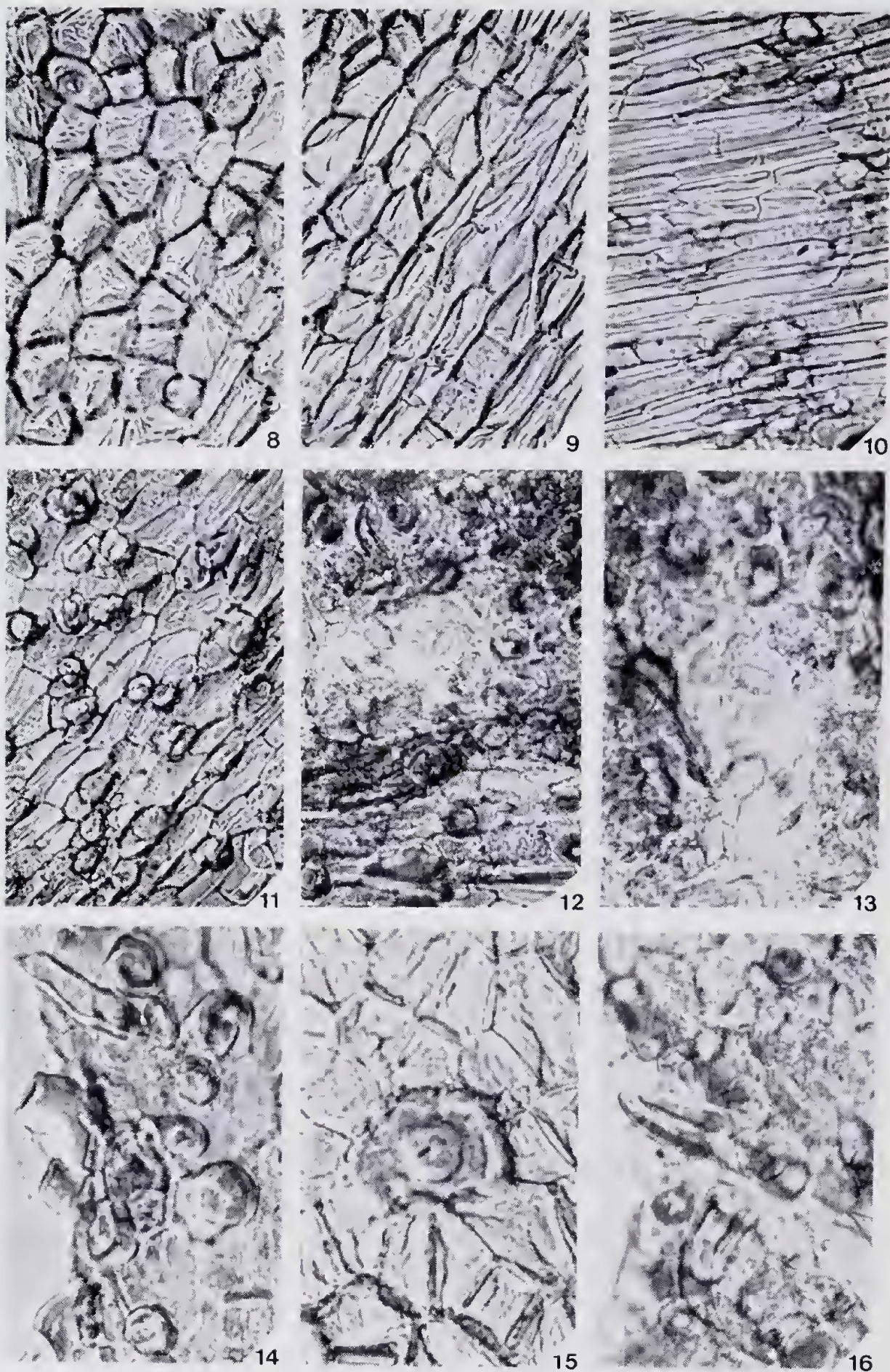
On the non-stomatiferous surface cell outlines are robust compact polygons with maximum dimension about 40 μm (Figs. 6, 8, 15). Those over veins tend to be elongate (Fig. 9). The cuticle within each outline shows a characteristic appearance of crease lines (Figs. 8, 15). Scattered sparsely are rounded polygonal cells each bearing a distinct, circular disc-like scar like that of a deciduous hair (Figs. 6, 8, 15). In no case does the scar lap the cell boundary. A further structure of which only one example was found consists of a group of cells of which the shared walls converge radially to a common fused centrum (Fig. 7). Cuticles of both surfaces have fine creasings and granulations which, like the appearance of the wall outlines themselves, defy ready terminology (Figs. 8, 11, 12).

Maslin Bay cf. Proteaceae II

Slides Maslin Bay cf. Proteaceae II, 1-8, Adelaide University Botany Department, see Figs. 17-19. The largest fragment embraces 1 cm of entire margin. The leaves are bifacial. The non-stomatiferous face is surfaced primarily with the one sort of unoriented cells of maximum dimension 15-35 μm . Walls are sinuous and between junctions have 1.5-2 waves of which the amplitude may approach the wavelengths but usually is less. On and near veins, walls are thinner and straight and outlines elongate. The cuticle lacks striation but has some indiscriminate punctation. The outstanding feature of the non-stomatiferous face is the striking appearance of the many complex hair bases (Figs. 17, 18). Each involves a discrete group of epidermal cells, typically 4-12 and commonly about 8, of which their collective perimeter is circular to ovoid tapered. Cell walls within this perimeter are thicker, straight and tend to meet at right angles with the overall appearance of a grille. Above the grille on the outer surface of the cuticle is the faint but definite scar of a deciduous hair. This scar shows up under interference phase contrast as the inner of two well-separated concentric circles or ovoids which are very finely drawn and lap all or most of the cells in the grille but not their collective



Figures 1 to 7.—Lake Lefroy cf. *Proteaceae* I. Drawings based on interference phase-contrast microscopy. 1.—Zone-diagram of the stomatiferous surface. 2.—Stomatiferous surface zone A; cell outlines of the central main vein. 3.—Stomatiferous surface zone B; cell outlines at the margin of the main vein; the dark circular outlines are the summits of papillae developed from small underlying cells. 4.—Stomatiferous surface zone C; cell outlines of the stomatiferous areas showing papillae, stomatal traces and a unicellular hair. 5.—Stomatiferous surface; two examples of the cuticle rolled to display trichomes in lateral view. 6.—Non-stomatiferous surface; inter-vein outlines including an example of the occasional cell with a deciduous hair scar. 7.—Non-stomatiferous surface showing the rare structure with walls of a group of cells radially convergent to a centrum.

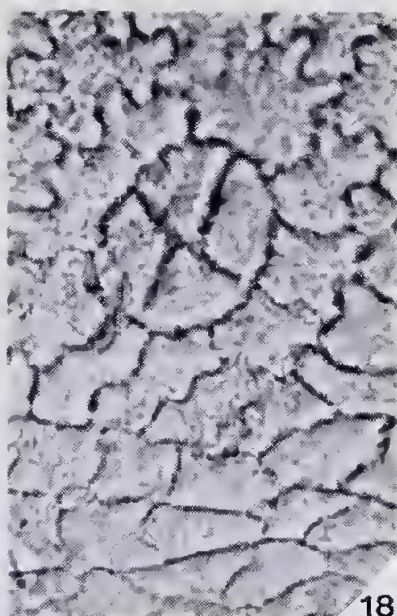


A
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┐
 50 μ m
┌
┐
 B

Figures 8 to 16.—Lake Lefroy cf. *Proteaceae* I. Monochrome photographs of cuticular fields which under interference phase-contrast microscopy involve colour contrasts. Figures 8-12 inclusive, scale A; Figures 13-16 inclusive, scale B. 8.—Non-stomatiferous surface showing the robust polygonal cell wall mesh, the characteristic cuticular creasing and occasional cells with a hair scar. 9.—Non-stomatiferous surface showing elongation of cell outlines over a vein. 10.—Stomatiferous surface showing the narrow parallel outlines of zone A with occasional papillae developed from interspersed short cells. 11.—Stomatiferous surface; cell outlines in zone B. 12 and 13.—Stomatiferous surface showing a stomatal trace both in context and in detail. 14.—Stomatiferous cuticle rolled to show trichomes in lateral vein. 15.—Non-stomatiferous cuticle showing a deciduous hair scar in detail. 16.—Stomatiferous cuticle rolled to show simple unicellular hairs among papillae.



17



18



19



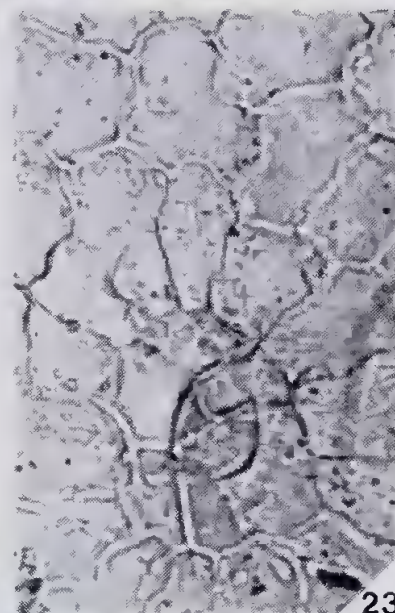
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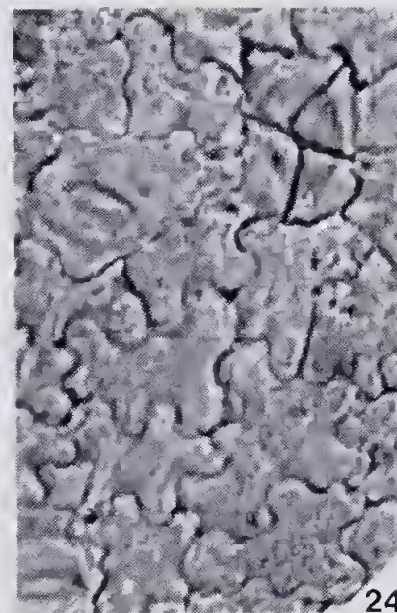
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23



24



25

50 μ m



Figures 17 to 25.—Monochrome photographs of cuticular fields which under interference phase-contrast microscopy involve colour contrasts. 17 to 19.—Lake Lefroy, cf. Proteaceae II. 17.—Non-stomatiferous surface showing pidermal cell outlines and a complex hair base with overlying scar. 18.—Non stomatiferous surface showing thinner, straighter walls near a vein. 19.—Stomatiferous surface showing stomatal trace, several hair bases and lengths of wavy wall. 20 to 22.—Lake Lefroy cf. Proteaceae III. 20.—Non-stomatiferous surface showing typical complex hair base and striae. 21.—Stomatiferous surface showing 1- and 2-celled hair bases, some joined; striae and stomates. 22.—Stomatiferous surface showing a large stomate with faintly-marked actinocytic surrounds; also the remains of a hair shaft on a 2-celled base. 23 to 25.—Lake Lefroy cf. Proteaceae IV. 23.—Non-stomatiferous surface showing tangled wall traces and hair base. 24.—Stomatiferous surface showing sinuous walls, complex hair base and stomata. 25.—Stomatiferous surface; lateral striae about the transverse stomatal slit in an elongated stomatal window.

perimeter. The maximum diameter of perimeters is 40-60 μm . They occur both on and between veins and average about 50/mm². Some are more or less linked by their narrow tapered ends.

The stomatiferous face has much thinner cuticle. Cell wall traces are marked only faintly and in places and fade out particularly near stomates. They are finer than on the reverse face and have up to five small irregular waves between wall junctions. They are most visible over veins where they are more or less straight, outlining elongate, oriented cells. Stomatal traces are extremely faint. Each is a circular to ovoid patch of smooth cuticle about 16 μm across with a central elliptical trace about 6 μm long. They appear anomocytic and unoriented at about 340/mm² (Fig. 19).

Hair bases average about 320/mm² on the stomatiferous face. Each has an outline 10-35 μm across enclosing a creased, more or less circular structure suggesting the attachments of a deciduous hair shaft. Some underlying outlines are unsectored but larger examples are sectored by thin straight walls either parallel, or intersecting at wide angles. On veins, delicate versions of the hair base characteristic of the non-stomatiferous face occur with a distinct ovoid scar overlying the grille. They are oval to elongate up to 35 μm , and some are linked in pairs by their narrow ends.

Maslin Bay cf. Proteaceae III

Slides Maslin Bay cf. Proteaceae III, 1-2, Adelaide University Botany Department, see Figs. 20-22. The fragments are bifacial. The non-stomatiferous face is surfaced primarily with uniform polygonal cells of 5-7 angles and maximum dimensions 15-35 μm . Walls vary from slightly crooked to lightly curved, sometimes in a flat sigmoidal curve. In places they fade out. Over expanses up to 0.5 cm², the largest available, there is no variation in cell shape or orientation to suggest veins. The outstanding feature of the non-stomatiferous face is the striking appearance of the many complex hair bases in combination with the bold cuticular striation which runs between them (Fig. 20).

Each base involves a discrete group of cells, from 2-14 but typically 4, of which their collective perimeter is a compact irregular outline 40-80 μm across, sometimes more or less circular to tapered ovoid but with angular indentations at wall junctions. Each base is picked out by the contrast between its smooth cuticle and the intervening cuticular surface which is boldly striate at about 7 parallel striae/cell width, running in unbroken patterns that converge on the smooth bases. Each base is sectored into an angular grille. A large ovoid scar of a deciduous hair is easily seen on the cuticle overlying the grille (Fig. 20). It consists of two concentric circles finely drawn, which lap all or most of the underlying grille cells but not their collective perimeter. Some still carry the hair which is based on the inner of the two circles and has a simple, unicellular, thin-walled shaft without ornament, about 70 μm long.

Cuticle of the stomatiferous face is thinner and primarily surfaced with angular polygonal cells of maximum dimension 20-30 μm in arrangements that tend to be actinocytic upon the numerous hair bases. Wall traces are thin, faint and break up, fading out into granulations among the striae which are finer, also fade out in places and do not describe the unbroken lines that characterize the reverse surface. They tend to be diffuse with local convergences on hair bases. There are two sizes of stomata which differ in numbers and arrangement but are otherwise similar. Each is enclosed by an oval to subcircular ring of the same fine wall that outlines general epidermal cells. This outline may be notched at the poles. Within this perimeter and separated from it by a band of thin smooth cuticle about 2-3 μm wide is a thick, smooth refractile band, oval in outline and about 4 μm broad. This encloses fine, smooth cuticle with a slit-like trace or crease over the long axis of the stomate. At each pole, projections from the perimeter wall extend inwards on the long axis across the thick band to the edges of the central slit.

Small stomates are scattered without orientation at about 270/mm². They are about 18 μm long and appear paracytic, with narrow curved lateral subsidiary cells, large epidermal cells abutting the poles and no convergent striae. Large stomates about 27 μm long and about 10/mm² are separated from the smaller by surrounds of epidermal cells of which the walls are very indistinct but sufficient to show that the large stomates lack narrow paracytic subsidiaries. Surrounding cells tend to wedge inwards against the stomatal perimeter in actinocytic pattern (Fig. 22).

Scattered among the stomates at about 120/mm² are hair bases. Some involve an angular to ovoid cell outline about 25-30 μm across enclosing the circular, creased base of a hair about 20 μm in diameter. Others involve an angular ovoid perimeter about 30-80 μm across with a single straight crosswall, lapped by the ovoid scar of a deciduous hair. These bases are sometimes joined in pairs by their narrow ends. Some still carry the hair which is a simple, unicellular, thin unornamented shaft about 40 μm long (Fig. 22), inserted on the inner ring of the scar. Less frequently the base consists of an ovoid to lenticular perimeter sectored into a grille of up to 7 or more cells, most of them lapped by the scar. Occasionally 2 or 3 lenticular bases are joined at their narrow ends.

Maslin Bay cf. Proteaceae IV

Slides Maslin Bay cf. Proteaceae IV, 1-7, Adelaide University Botany Department, see Figs. 23-25. The fragments are bifacial and the greatest length of margin represented, 1.5 cm, is entire. The non-stomatiferous face is surfaced with cells about as long as wide and of similar size, about 18-25 μm . Their walls show the enigmatic condition illustrated by Lange (1969b, fig. 10), i.e. they are like cords which loop across each other, tangle, fuse and sometimes show free projecting ends (Fig. 23). Outlines are thus

more or less square to polygonal with erratic inuosities and looped double strands in places. Over areas up to 1.5 cm² (the largest available) the pattern shows no veins. The cuticle is indiscriminately punctuate and in places shows fine striae converging on occasional hair bases.

Hair bases are scattered sparsely at about 0/mm². Each involves a group of 2-5 epidermal cells, commonly 4, with a collective perimeter roughly circular, ovoid or lenticular 30-50 µm across. Internal walls describe an untidy sometimes tangled grille. Over the grille is a circular to ovoid hair scar which laps most cells but not the perimeter.

The stomatiferous face has thinner cuticle. It is primarily surfaced with non-oriented uniform cells about 20-40 µm across with fairly regular sinuous outlines. Walls between junctions have 1.5-2 waves of sinuosity of which the amplitude is about half the wavelength (Fig. 4). In places the wall traces loop and tangle. Scattered among the general epidermal cells are stomates, complex hair bases and occasional lesions ringed by a converging pattern of many cells and interpreted as a malformation due to ungual parasitism. The stomates are very characteristic. Each occupies a window of extremely thin, delicate, creased cuticle 25-35 µm across which appears to supplant an ordinary epidermal cell and is highlighted by its transparency relative to surrounding cuticle. Transverse to the long axis of the window is an ellipse about 6-9 x 16-18 µm which is thick walled and encloses a clear central area. In many cases a pattern of creases runs from the sides of the ellipse to the ends of the window (Fig. 25). Stomata occur at about 160/mm² and are not oriented.

The hair bases are discrete groups of cells of which the collective perimeter is usually ovoid, up to 55 µm across. Straight walls either transverse, or intersecting at wide angles, describe a grille, above which lies the scar of a deciduous hair.

Comparisons with Proteaceae

Lake Lefroy cf. Proteaceae I

Each cuticular feature of this form finds ready matches among living Proteaceae at least as a clearly-related version of a condition well represented in the family. The same applies to progressive combinations of features, up to the case where the total combination is embraced by a particular living genus, but no single species, of Proteaceae.

When the fossil is compared with cuticles from the range of Proteaceae listed earlier only *Banksia*, *Dryandra* and *Synaphea* appear to accommodate its fundamental combination of characteristics, namely: bifacial leaves with thin stomatiferous and thicker non-stomatiferous cuticles, the non-stomatiferous with only robust polygonal cell outlines, characteristic cuticular wrinkling and occasional cell outlines bearing the distinctive scar of a deciduous hair; lateral venation leaving the main vein at right angles and closely spaced to enclose stomatiferous cuticle into many rounded patches; those

patches bearing many trichomes and stomatal traces which consist of thin translucent areas surrounded by thicker cuticle and exhibiting a delicate elliptical slit-like central trace.

Between *Banksia* and *Dryandra* on the one hand and *Synaphea* and the Lake Lefroy fossil on the other, various features discriminate. *Synaphea* and the Lake Lefroy fossil both exhibit papillae and unicellular hairs interspersed. *Banksia* and *Dryandra* do not. They have bicellular hair shafts of a distinctive sort which, so far as is illustrated from fossils (Cookson and Duigan 1950), never break off to leave basal cells at all like the papillae of the Lake Lefroy fossil; instead they leave bases which are torn at the summit. In addition, hair scars on *Synaphea* and on the Lake Lefroy fossil are always contained within one epidermal cell outline whereas on many *Banksia* and *Dryandra* hair scars lap more than one epidermal cell.

Maslin Bay cf. Proteaceae II, III and IV

All cuticular features of each of the three forms find matches among living Proteaceae either as an indistinguishable match, a very close resemblance or as a version of a condition represented in the family. The degree to which progressive combinations of the fossils' characteristics leads to exclusive matches within Proteaceae varies between the three forms. Maslin Bay cf. Proteaceae III has features of which the comparison of progressive combinations eliminates all but *Darlingia* and *Knightia* with the weight of similarity to *Darlingia*, which exhibits the same stomatal appearance in detail, the same variations in stomatal size, the same form of paracytic subsidiaries, the same variability in strength of cell wall trace, similar striae and the same sorts and variety of hair bases on the stomatiferous surface. It differs by having more or less straight walls whereas *Darlingia* has sinuous walls. *Knightia* matches less well, lacking paracytic subsidiaries or variety of stomatal size. The non-stomatiferous surface of the fossil similarly indicates *Darlingia*.

Forms II and IV are not so tractable. The stomatiferous surface of form II indicates *Helicia* in respect of the characteristic hair bases, faint wall traces with many small waves, and round anomocytic stomates in the particular arrangements presented, but reference to the non-stomatiferous surface while strengthening evidence for Proteaceae, leads away from *Helicia* back towards genera such as *Darlingia*. Form IV is the most intractable. For example its transverse elliptical stomatal slits bisecting translucent cuticular windows and with flanking striae find parallels in *Finschia*, its rather delicate and crumpled complex hair bases in *Helicia*, its tangled net-like wall traces in *Grevillea*, and so on, but a substantial combination of its characters were not found in any of the comparison genera.

Discussion

It was hoped that particular living vegetations might show up as rich matching sources for Australian Eocene fragments, but none did. The probability of a highly-distinctive close match

between arbitrarily-drawn fossil and living fragments (at or near the species level) was very remote ($p < 0.00001$).

It took ten years to accomplish the 2.4 million comparisons involved in this study. This does not encourage the idea that an Australian assemblage of Eocene angiosperm leaf-fragments (too fragmentary to convey leaf macromorphology) is likely to be elucidated as to its botanical affinities with living species simply by making a large number of arbitrary direct comparisons.

Nonetheless instances of distinctive close comparability can be detected by the approach and it is simple if laborious in some cases then to specify that the match is exclusive within certain limits, e.g. to 0.2% of genera in a large random sample of Australian region angiosperms.

If arguments are to be pursued about phyletic relationship between forms thus matched (with ascription of the fossil to the taxon of the living comparison material) the question is whether such demonstration of exclusiveness is adequate. Here the issue is not whether the demonstration convinces the investigator but whether it will convince taxonomic botanists in general and the Australian experience is that the latter expect very rigorous demonstration. Clearly, it would be mere sciolism to ascribe the fossil outright to the first match detected.

Thus in the course of this study, complex hair bases as in Fig. 20 were for a long while observed only from Proteaceae. When seen in leaf-litter samples from widely-scattered vegetations (Lange 1976) back-checking to the source plant invariably led to Proteaceae regardless of whether the litter came from Tasmania, New Zealand or mainland Australia. Subsequently a very similar hairbase was detected from Araliaceae of New Guinea and a related structure from northern hemisphere *Platanus*. Similarly papillae as in Fig. 14, long observed only from Proteaceae, were detected in Barringtoniaceae as comparisons widened.

There seems to be no limit to the comparisons that might be deemed adequate to specify the exclusiveness of a match. The ascription of northern hemisphere Cretaceous fragments to the phyletic lines of living Australian and New Zealand genera (Rüffle 1965) illustrates how cuticular analysts already regard global flora as potential comparison material.

Fossil fragments could not be matched and specified as to their exclusiveness more readily at the family than the species level. Many families tend to be very heterogeneous in cuticular characteristics. Some Proteaceae have nothing cuticular in common with others and instead resemble species in other families.

Essentially, the approach examined in this paper tends to founder on the disproportion between available and necessary comparison data and on the immense work necessary to bridge the gap.

The Western Australian fossil which resembles *Synaphea* provides first indications from leaf-cuticles for the presence in Palaeogene floras of any of the endemic Western Australian Pro-

teoideae, or the subfamily itself. The South Australian fossils include evidence for *Darlingia*, which is very close to *Knightia*. This reintroduces the question of these genera in Palaeogene floras following refutation by Dilcher and Mehrotra (1969) of some earlier claims for *Knightia*.

As matters stand, this evidence must remain at a face value that cannot be upgraded without much wider studies of living angiosperm cuticles. It is strong evidence, but not yet enough to allow ascriptions to the living genera without significant risk of sciolism, or to convince rigorous botanists.

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An ecological reconnaissance of four islands in the Archipelago of the Recherche, Western Australia

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Manuscript received 20 September 1977; accepted 25 October 1977

Abstract

In 1976 Woody and Mondrain Islands, and in 1977 Wilson, Mondrain and Salisbury Islands were visited for between 1 and 14 days. Lists and, where necessary, collections were made of molluscs (Mondrain I.), plants (all islands), reptiles (Woody I., Mondrain I.), birds (all islands), and mammals (all islands). Many new records for the islands were found: those new for the Archipelago are molluscs (20 species), plants (13 species), reptiles (3 species) and birds (3 species).

Quantitative estimates of abundance of certain land bird species (Woody I., Mondrain I., opposite mainland) show that the two most abundant bird species on Woody and Mondrain Is. were also the two most abundant species in the most comparable mainland habitat studied. Vegetation maps for Woody and Mondrain Is. show the extent of various habitat types and the areas of the dominant plant species. The development of plant communities in terms of exposure and density of burrowing seabirds is discussed.

It is argued that these islands are too large to allow accurate assessment of turnover for plants or reptile species. Turnover is, however, minimal or nonexistent for land birds and mammals.

Island area *per se* and the presence of rock piles probably do not account for the presence of Rock wallabies on only four islands. A new hypothesis is proposed relating their presence on some of the outer islands to more predominant halophytic elements in the floras of the outer islands.

Introduction

The floras and faunas of islands have given impetus to the development of theories of speciation, coexistence of species and lately the design of reserves on mainland areas (Main and Cadav 1971). Isolation is associated not only with faunas and floras poor in species, but also with non-random samples of species composition of the fauna and flora on the adjacent mainland. The results are shifts in abundance of various species, leading to different coadapted species complexes from on the mainland.

Islands, particularly small ones, allow the possibility of complete enumeration of vertebrate and plant species. This is rarely realized on mainland sites because there are always some species in such low numbers that they are overlooked. More importantly, delineation of the shape and size of mainland sites is usually artificial. Islands therefore offer the advantage that if baseline studies are thorough enough, subsequent visitors will have a yardstick with which to monitor changes, if any, in the occurrence or abundance of species.

Although many islands around Western Australia have been surveyed, visits have been short (often one day) and lists produced deal with

at best only a few taxa. Storr (1965) seems to have been the first to pay attention to an ecological reconnaissance of the flora and vertebrate fauna of Western Australian islands. He provided annotated lists and discussion of the vegetation types, flora, reptiles, birds and mammals present on some islands in Houtman Abrolhos. In our opinion, his paper could only have been improved upon by quantifying the abundance of the species on his lists.

In this paper we provide new or detailed information on the vegetation types, plant, reptile, bird and mammal species on four islands in the Archipelago of the Recherche (Fig. 1). In some cases we provide quantitative estimates of abundance of bird species (Mondrain I., Woody I.), macropod species (Mondrain I., Woody I., Wilson I., Salisbury I.) and reptile species (Mondrain I.). A list of additional molluscs found on Mondrain I. is also given. Where possible comparisons are made with the adjacent mainland and other Recherche islands (Fig. 1).

Previous research

Members of the Australian Geographic Society expedition of November 1950 made the first concerted attempt to compile lists of the

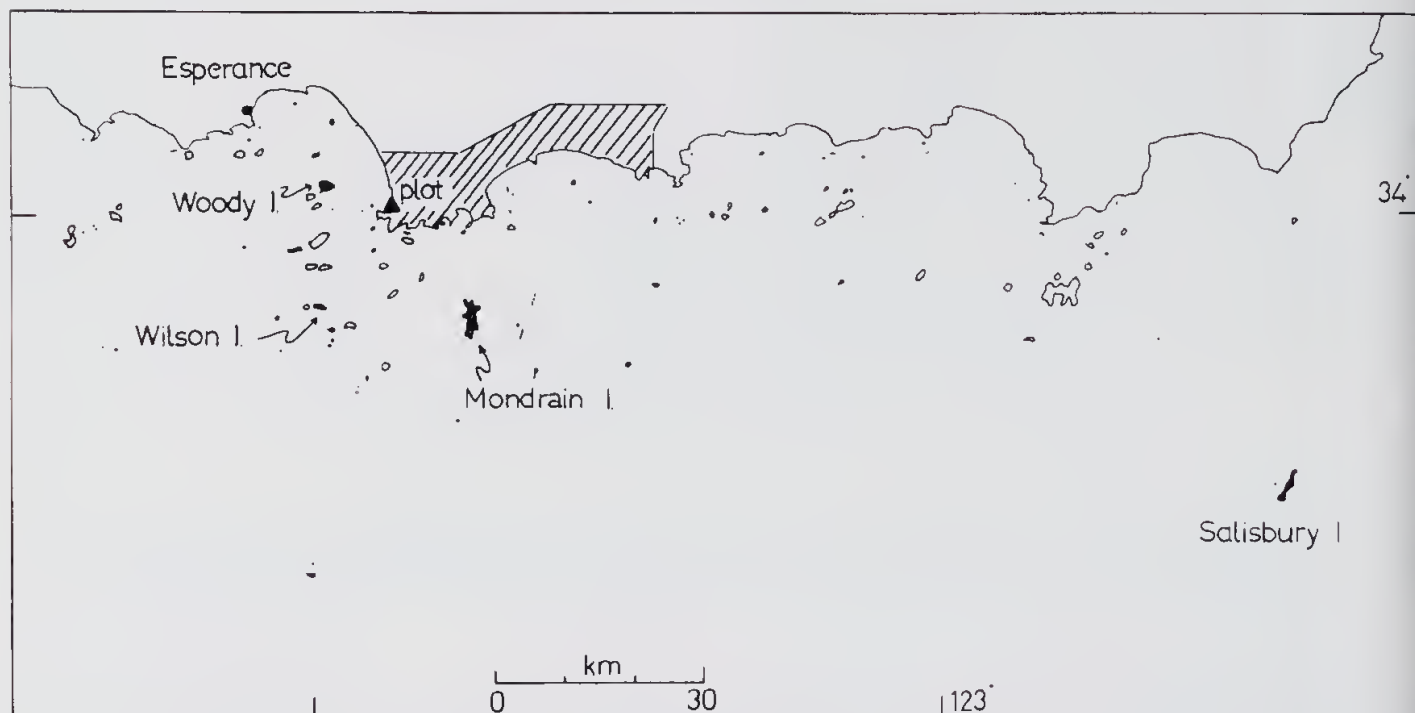


Figure 1.—Map of part of the Archipelago of the Recherche showing the 4 islands, the mainland plot at the east end of Esperance Bay, and Cape Le Grand National Park (shaded area).

flora and fauna for 20 islands, including three (Mondrain, Woody and Salisbury) of the four we visited. Goodsell *et al.* (1976) re-collected on Woody I. over nine days in spring 1975. Nothing has been published on the fauna or flora of Wilson I., though it has long been known that this island has a population of Rock wallabies (Serventy 1953).

Details of our visits

Period of time spent on the islands was as follows: Woody I., 3-16 February 1976; Mondrain I., 16-29 February 1976, 25-27 April 1977; Wilson I., 7 hr. on 25 April 1977; Salisbury I., 3 hr. on 28 April 1977. Black and Abbott worked together on Mondrain in February 1976; otherwise collections and observations were made by Abbott.

Salisbury alone of these islands has limestone present, as a thick aeolianite capping over the whole island except the southern end. The islands are basically granitic-gneissic, and are made up of domes and finger-like projections. For a recent discussion of the geomorphology of such islands, see Twidale (1971).

Plant species

Woody Island (188 ha, 130 m high)

Willis (1963) collected 85 species on 30 November 1950 from the northern side of this island, only about 10 months after a fire had swept over the island. Twenty five years later, Goodsell *et al.* (1976) spent 9 days on the island and collected 121 plant species. Willis recorded 28 plant species that Goodsell *et al.* did not collect. How many of these species actually became extinct in the intervening years? Seven of these

species actually represent name changes or different opinions about the names of plants collected in 1950 and 1975. These are *Poa cacspitosa*, *P. porphyroclados* (the first name is the one used by Willis (1953); the second that of Goodsell *et al.* (1976)); *Stypandra imbricata*, *S. ?glauc*; *Rhagodia radiata*, *R. baccata*; *Crassula miriamae*, *C. colorata*; *Leucopogon obovatus*, *L. revolutus*; *Gnaphalium involucreatum*, *G. sphaericum*; *Sonchus oleraceus*, *Sonchus* species. Of the remaining 21 species, 14 were collected in February 1976. These were *Bromus arenarius*, *Polypogon monspeliensis*, *Scirpus antarcticus*, *Centrolepis strigosa*, *Tetragonia amplexicoma*, *Spergularia rubra*, *Gastrolobium bilobum*, *Medicago hispidula*, *Frankenia tetrapetala*, *Apium prostratum*, *Platysacc compressa*, *Trachymene pilosa*, *Myoporum adscendens* and *Cotula cotuloides*. The remaining 7 species which have not been recorded since Willis' visit are indicated in Table 1A. It seems possible these species are now extinct on Woody I., but given the large size of the island they may simply have been overlooked. Future botanical visitors should look out for these 7 species.

Excluding the 7 species listed above that are probable taxonomic equivalents, Goodsell *et al.* (1976) from their examination of the whole island collected 54 species new to the island, many of which are new records for the Archipelago. Thirty of these species were recollected in February 1976. The remaining 24 are listed in Table 1A. Subsequent visitors should especially search for these.

However, in February 1976, 27 species not collected by Willis or Goodsell *et al.* were found on Woody I. (Table 1B). Nine of these are new records for the Archipelago. In all, the total number of species collected from Woody I. is

70 species, which means that this island has the highest plant species/area ratio yet known in the Archipelago. Willis (1953) had suggested that Sandy Hook I. was the most floriferous island in the Archipelago; this could still be so as Willis specifically states that his collecting here was incomplete.

Mondrain Island (787 ha, 226 m high)

The parts of this island covered by Willis and by us are shown in Fig. 2. Clearly, parts of this large island have not been traversed,

so that the list of the flora of Mondrain I. must still be considered incomplete. Subsequent visitors should attempt to traverse different parts of the island.

Willis (1953) recorded 40 species that we did not find (Table 2A); in contrast we were only able to add 17 species not listed by Willis for the island (Table 2B). Three of these are new records for the Archipelago. In addition, the *Dryandra* species collected by Willis but not identified to species has been determined as *D. longifolia* R.Br. from our material (A. S. George,

Table 1

Plant species collected on Woody Island

Species collected by Willis, November 1950 (W) or Goodsell, October-November 1975 (G) but not by Abbott, February 1976.

**Bromus hordeaceus* W, G
**Cynodon dactylon* W
**Hordeum marinum* W
**Vulpia bromoides* W, G
**V. membranacea* W, G
Lepidosperma sp. G
L. tuberculatum G
Juncus bufonius W
J. plebeius W
Thysanotus dichotomus G
T. patersonii G
Prasophyllum sp. G
Portetaria debilis W, G

Dryandra nivalis G
Petrophile teretifolia G
**Cerastium glomeratum* W
Bossiaea dentata G
**Trifolium campestre* G
**T. tomentosum* G
Geranium solanderi G
Pelargonium littorale G
Comesperma confertum G
Trymalium spathulatum G
Eucalyptus sp. n. G
McLaleucas sp. G

Leucopogon parviflorus G
Myoporum tetrandrum G
Wahlenbergia ? gracilentia G
Dampiera ? coronata G
Scarcia aemula W
Stylidium adnatum G
S. glandulosum G
**Arctotheca populifolia* W, G
Cotula coronopifolia G
Ixiolaena viscosa W, G
Stuartina muelleri W
Waitzia citrina G

Species collected by Abbott, February 1976 but not by Willis, November 1950 or Goodsell, October-November 1975.

Sporobolus virginicus
†*Danthonia ? setacea* (not caespitosa)
**Lolium loliaceum*
**Vulpia myuros*
Lepidosperma viscidum
Juncus maritimus
**Rumex crispus*
**Chenopodium murale*
**C. pumilio*

Threlkeldia diffusa
Lepidium foliosum
†**Erodium cicutarium*
Boronia albiflora
Comesperma volubile
Stackhousia heugelii
Dodonaea oblongifolia
Spyridium spadicum
Leucopogon apiculatus

Dampiera prostrata
Stylidium pilosum
†*Vittadinia graveolens*
†**Gnaphalium candidissimum*
Angianthus humifusus
A. tenellus
†*Quinetia urvillei*
†*Carduus tenuiflorus*
Calocephalus brownii

* Naturalized alien species.

† New record for Archipelago.

Table 2

Plant species collected on Mondrain Island

Species collected in November 1950, but not in February 1976.

**Polypogon monspeliensis*
Bromus arenarius
**Briza minor*
Anguillaria dioica
Agrostoides scabrum
Thysanotus patersonii
T. dichotomus
Patersonia inaequalis
Microtis unifolia
Catadenia latifolia
Muehlenbeckia adpressa
Calandrinia calypttrata
Lepidium foliosum
Drosera glanduligera

D. macrantha
Crassula bonariensis
Acacia crassiuscula
Chorizema aciculare
Gastrolobium knightianum
Templetonia retusa
Oxalis corniculata
Comesperma volubile
C. confertum
Hibiscus heugelii
Rulingia grandiflora
Hydrocotyle alata
Leucopogon gnaphalioides

Sebaea ovata
Westringia dampieri
**Solanum nigrum*
Galium australe
Wahlenbergia gracilentia
Goodenia scapigera
Lechenaultia formosa
Dampiera lavandulacea
Stylidium brachyphyllum
Levenhookia pusilla
Cotula coronopifolia
C. australis
**Hypochoeris glabra*

Species collected in February 1976, but not in November 1950.

Sporobolus virginicus
†*Schoenus ? subflavus*
Lepidosperma gladiatum
Gahnia trifida
Lomandra rigida
Atriplex cinerea

†*Rhagodia preissii* Moq.
Cakile maritima
Acacia cyclops
Phebalium rude
**Euphorbia paralias*
†*Melaleuca radula*

†*Acrotriche aff. ramiflora*
Leucopogon apiculatus
L. interruptus
Lobelia heterophylla
Dampiera prostrata
Angianthus humifusus

* Naturalized alien species.

† Species new to Archipelago.

pers. comm.). Dr. Willis has pointed out that his record of *Leptomeria cunninghamii* is a misidentification for *L. empetriiformis* Miq. The total number of plant species now recorded for Mondrain I. stands at 156.

Wilson Island (123 ha, 80 m high)

R. D. Royce (unpubl.) collected 32 species on Wilson I. on 1 February 1960. Forty species were collected on 25 April 1976 (Table 3). However, 9 of Royce's species were not found by Abbott. These are *Microtis* species, *Verticordia minutiflora*, *Haloragis* species, *Centaureum spicatum*, *Apium prostratum*, *Cotula coronopifolia*, *Gnaphalium* 2 species, and *Sonchus oleraceus*. This island needs to be visited in spring.

Salisbury Island (316 ha, 119 m high)

No botanist has yet collected over the whole of this island. Willis (1953) recorded 25 species, and Abbott failed to find 7 of these: *Parietaria debilis*, *Crassula miriamae*, *Salicornia blackiana*, *Tetragonia amplexicoma*, *Muehlenbeckia adpressa*, *Clematis pubescens*, and *Apium prostratum*. Three species, not listed by Willis, were found: *Dianella revoluta*, *Disphyma blackii*, and *Acacia rostellifera*. However, although *D. blackii* is not in Willis' systematic list, on p. 19 he does state that this species was present on every island visited in 1950. An *Atriplex* collected on this island has been determined as *A. paludosa* sub-species *baudinii* Aellen (P. G. Wilson pers. comm.), so that it is possible that Willis' *A. cinerea* is a misidentification.

Vegetation

Vegetation maps are provided for Woody and Mondrain Islands (Figs. 3, 4). Insufficient time was spent on Wilson and Salisbury Is. to attempt mapping. The maps are a mixture of the key plant species and structural components if no one species could be recognized as dominant.

Woody Island

Goodsell *et al.* (1976) provide a map of vegetation zones based purely on structural criteria, mainly height and canopy cover. We recognized six classes (Fig. 3). The two main ones are low open-heath on the western half of the island and *Eucalyptus*-dominated closed-forest on the sheltered slopes south and east of the summit. Four *Eucalypts* are present, *E. cornuta* and *E. lehmannii* in exposed places (to 5 m), *E. platypus* var. *heterophylla* (to 10 m) in the closed-forest and *E. angulosa* (to 2 m) scattered throughout open-heath.

The open-heath has an average height of 1-2 m, and closely resembles vegetation of the gentler slopes and plateaux around Mt. Le Grand on the adjacent mainland. It was from this habitat on Woody I. (not investigated by Willis) that the list of plants for Woody I. was increased by half by Goodsell *et al.* (1976). Predominant species are: *Dampiera prostrata*, *Boronia albigera*, *Lepidosperma leptostachyum*, *L. viscidum*, *Gahnia trifida*, *Calothamnus quadrifidus*, *Iso-pogon trilobus* and *I. formosus*, *Hakea trifurcata*, *Gastrolobium bilobum*, *Hibbertia* aff. *acerosa*,



Figure 2.—Areas of Mondrain Island traversed by Willis in 1950 and by Abbott and Black in 1976 and 1977. x and y are the landing places and camp sites in 1950 and 1976-7.

and *Leucopogon rotundifolius*. This habitat is associated with rocky areas with little soil. Burrowing seabirds are absent from such areas, so that levels of phosphorus and nitrogen are probably as low as on similar habitats on the mainland. This habitat is well developed on the central plateau of Mondrain I. (see below) and the southwest part of Bald I., east of Albany.

Melaleuca lanceolata occurs above the shoreline around most of the island, and with *Astartea fascicularis* forms closed-heath intergrading into closed-scrub where sheltered from the southwest. *Acacia acuminata* var. *latifolia* forms stands of closed-heath or closed-scrub, mainly on deeper soils on sheltered parts of the island, and occasionally *Melaleuca elliptica* and

Table 3
Flora of Wilson Island (collected 25 April 1977)

Sporobolus virbinicus
Stipa sp.
Poa australis agg.
Scirpus nodosus
Centrolepis strigosa
C. polygyna
Lomandra rigida
Hakea clavata
H. suaveolens
Muchlenbeckia adpressa
Atriplex ? *paludosa* subsp.
 baudinii
Rhagodia ? *crassifolia*
Enchylaena tomentosa

Threlkeldia diffusa
Carpobrotus virescens
Disphyma blackii
Tetragonia amplexicoma
Eutaxia obovata
Bossiaea dentata
Pelargonium australe
Dodonaea oblongifolia
Phyllanthus scaber
Beyeria viscosa
Stackhousia huegelii
Rulingia cygnorum
Pimelea clavata
Eucalyptus cornuta

Agonis marginata
Leptospermum sericeum
Melaleuca globifera
Astartea fascicularis
Platysace compressa
Andersonia sprengelioides
Leucopogon obovatus
* *Solanum nigrum*
Myoporum adscendens
Stylidium adnatum
Olearia axillaris
Calocephalus brownii
Senecio lautus

* Naturalized alien species.

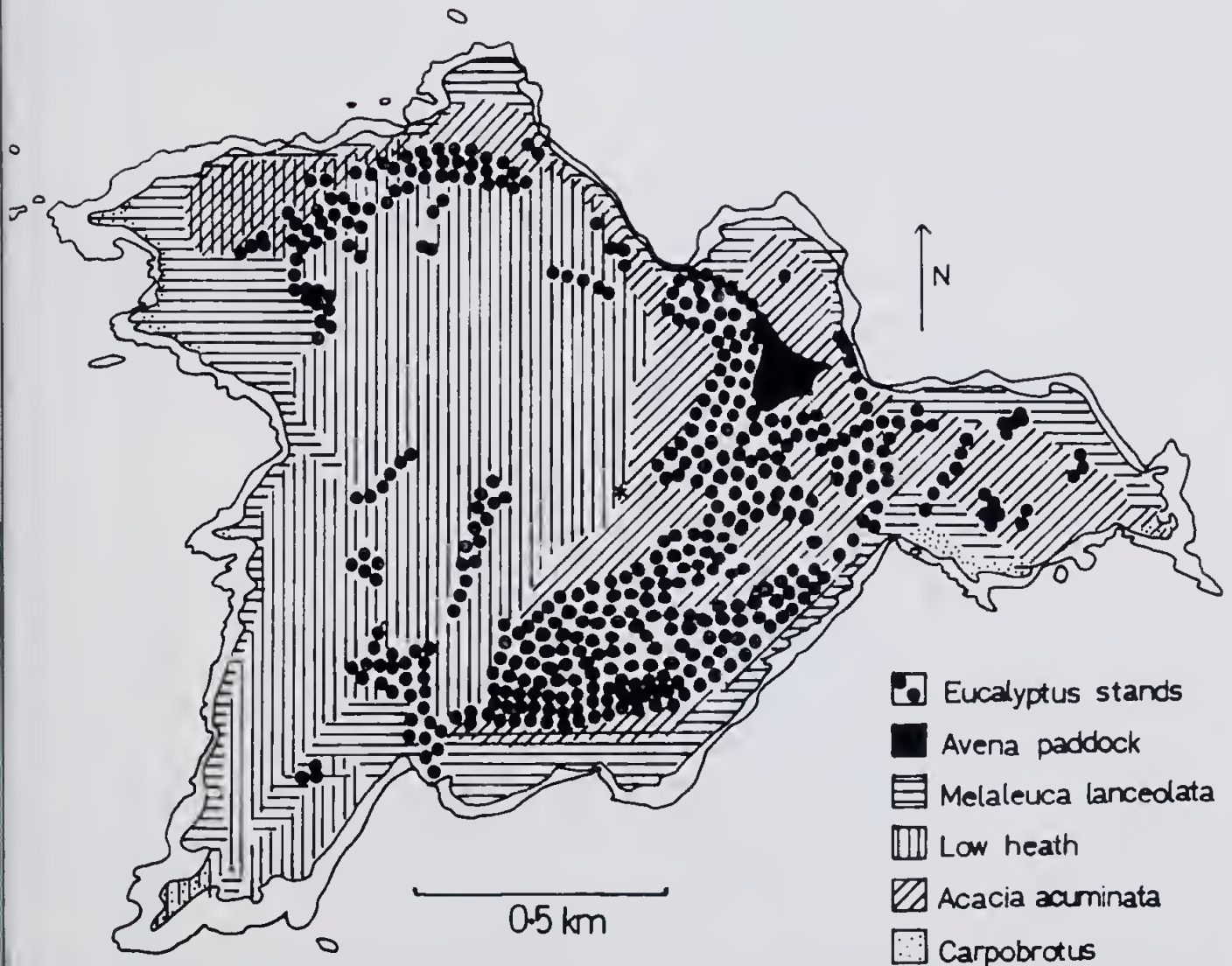


Figure 3.—Vegetation map of Woody Island, February 1976. * denotes summit. White areas represent (at this scale) bare rock.

Acacia myrtifolia mix with it. Rock ledges throughout the island are usually fringed with *Anthocercis viscosa*, *Hakea suaveolens* and *Agonis marginata* (all to 2 m) and *Platysace compressa* (to 1 m).

In April we flew over all the islands in Esperance Bay at low altitude, and we are convinced that of these islands Woody I. has the most diverse vegetation. There is a small paddock of *Avena barbata* (apparently misidentified as *A. fatua* by Willis) which is being encroached on by bushes of *Albizia lophantha*, *M. elliptica* and *Lycium ferocissimum*.

Mondrain Island

In contrast to Woody I., the major community on Mondrain I. is dominated by *Melaleuca globifera*, a species that does not occur on Woody I. even though it is common on the adjacent mainland coast. *M. globifera* is associated with *Bossiaea dentata* and *Acacia acuminata* to form 2-3 m high closed-heath or closed-scrub. Patches of Eucalypts occur as closed-scrub (in exposed places) grading into low closed-forest on deeper soils. The dominant species is *E. lehmannii*. *E. angulosa* (as on Woody I.) is common amongst the open-heath and open-scrub on the central plateau (Fig. 4). *E. platypus* and *E. cornuta* were rare. The flora of the open-heath resembles that of the hills around Mt. Le Grand, and not sand-plain as suggested by Willis (1953). The heath is quite open on the shallow soils of the rockier western part of this plateau, but on the eastern side is dense, to 2-3 m. Conspicuous species are: *Dryandra longifolia*, *Eucalyptus angulosa*, *Lepidosperma angustatum*, *Loxocarya flexuosa*, *Xanthorrhoea preissii*, *Casuarina trichodon*, *Boronia albiflora*, *Dodonaea oblongifolia*, *Hibbertia* aff. *acerosa*, *Calothamnus quadrifidus*, *Lcucopogon rotundifolius*, *Gastrolobium bilobum* and *Acacia nigricans*.

Melaleuca lanceolata occurs either as closed-heath on exposed areas or, away from the coast, as low closed-forest under which muttonbirds burrow. Large breaks of *Carpobrotus virescens* herbfield develop in such places. However, *Carpobrotus* and other succulents are most abundant close to the coastline, where *Sporobolus virginicus*, *Disphyma blackii*, *Calocephalus brownii*, *Rhagodia baccata*, and *Atriplex cinerea* merge into wind-pruned *Astartea fascicularis* thickets. Closed tussock-grassland is best developed at the extreme south end.

Around the peaks on the island, *Melaleuca globifera* is still dominant but the usual species of soil pockets around rock slabs (as at Woody I.) are present, including *Kunzea baxteri*, *Casuarina huegeliana*, *Borya nitida* and *Lomandra rigida*.

The extensive fires on both Woody and Mondrain (burnt as early as 1802) Islands seem to have had surprisingly little effect, although we have no accurate knowledge of the original vegetation prior to the frequent firing. On Middle I., the largest island in the Archipelago, Willis (1953) reported *Eucalyptus* forest over 10 m tall, and he found comparable examples in the southeast valley on Mondrain. It is regret-

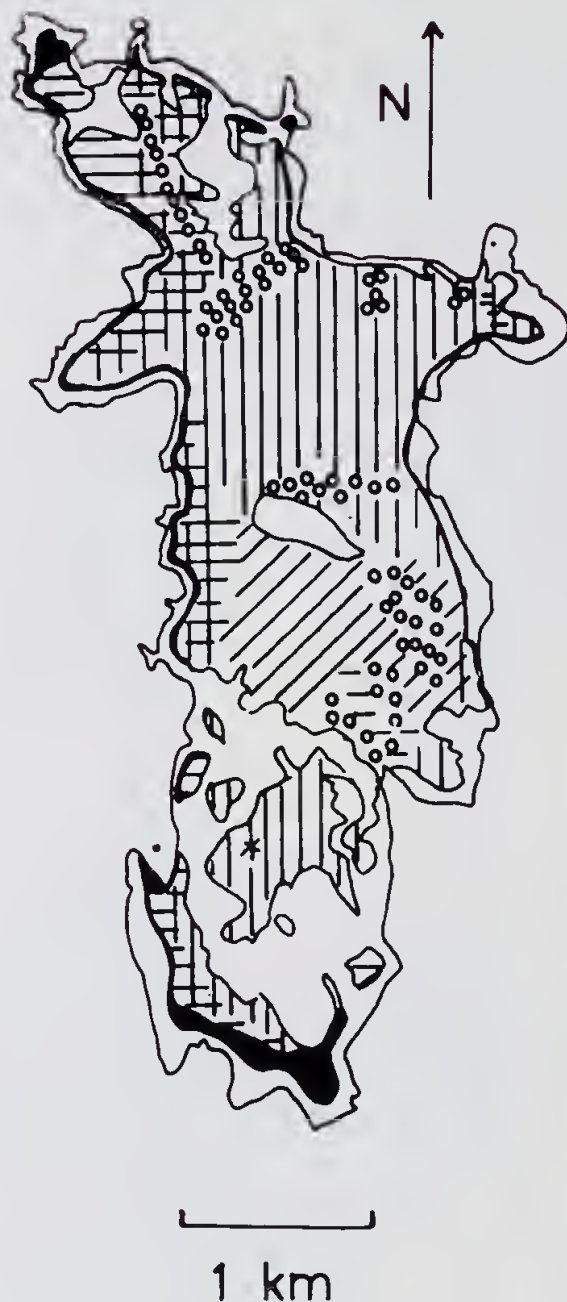


Figure 4.—Vegetation map of Mondrain Island, February 1976. * denotes summit. White areas represent (at this scale) bare rock.

table that analyses of the kind made by Symon (1971) on Pearson Island, South Australia cannot be carried out on any Recherche island.

On Woody I. the *Eucalyptus platypus* stands are even aged, thin bodied, and reach 10 m. The original stand was probably of similar height but with trees more widely spaced as on Middle I.

Beard (1975) claimed that the freedom from fire on the islands is of importance in the development of the distinctive island plant communities. However, degree of exposure and the presence of breeding seabirds are at least as important, if not more so. It is the rocky areas on the west or central parts of Woody I., Mondrain I. and elsewhere on Bald I. which seabirds find unsuitable for burrowing that have a flora most resembling the mainland one. Three main factors seem to govern the development of the various plant communities: degree of exposure, type of rock (and soil properties) and presence and density of seabird populations. The relationship of these factors on the Recherche islands is outlined in Fig. 5. The major effect of seabirds on these islands is different from other islands around southwest Australia. The Black-faced Cormorant breeds on one small spot on one island only, and surface-nesting species (Crested Tern, Silver Gull) do not form large colonies. However, five species of burrowing seabirds are widespread (Serventy 1952).

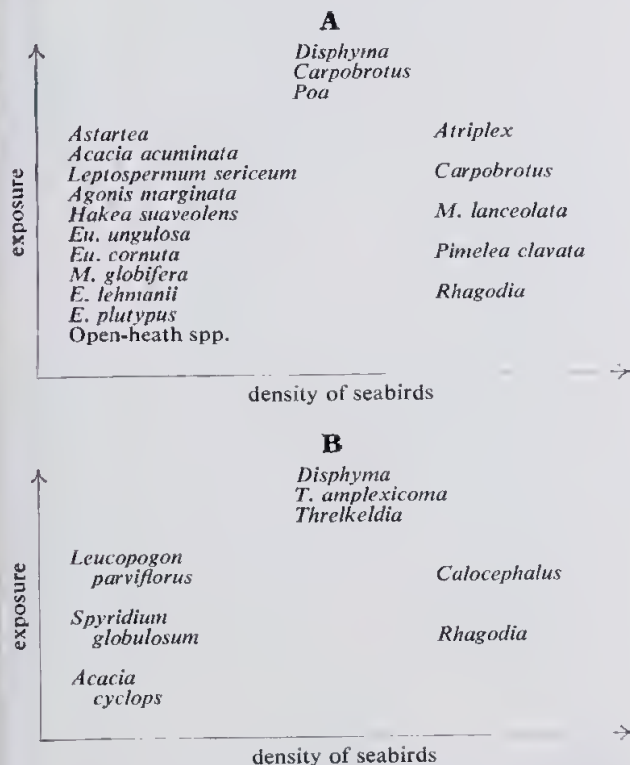


Figure 5.—Relation of dominant elements in vegetation of Recherche islands to exposure (wind, sea spray) and density of breeding sea birds; A.—on soils derived from granite; B.—on soils derived from limestone.

Wilson Island

This island consists of a high (68 m) eastern dome connected by a saddle to a higher dome (80 m) from which a mass of rock projects westwards. On this exposed western projection,

vegetation is planed and consists of *Carprobrotus* and *Disphyma* herbfield with occasional low bushes of *Astartea fascicularis*, *Calocephalus brownii* and *Myoporum adscendens*. On the lee side of both peaks patches of *Melaleuca globifera*, *Astartea*, *Agonis marginata* and *Leptospermum sericeum* (2-4 m) occur and there is one small area of *E. cornuta* (2.5 m) behind the 80 m peak. An extensive *Atriplex* plain, burrowed by shearwaters, occurs on the northern slopes of the finger-like part of the island.

Salisbury Island

We can add little to the description given by Willis (1953). The steep northern slopes have vegetation to 1 m and closely resemble those on Michaelmas I. near Albany, though there are differences in plant species present. On the plateau, which consists of weathered aeolianite that is a remnant of old dune deposits formed when the sea was lower, the vegetation reaches 1-2 m and is very wind-pruned.

Molluscs

Following the method of the 1950 expedition of the Australian Geographic Society, we collected "beach-worn specimens, the value of which as a basis for a survey is limited" (Macpherson 1954, p. 55). Nevertheless our collection of dead shells from the sandy shell beaches of Mondrain I. revealed 28 species not recorded for the island previously, of which 20 species are new to the Archipelago (Table 4). We also made extensive collections of living molluscs from accessible intertidal shores around the landing place (northeast cove), and in addition to the living specimens of the species indicated in Table 4, we found living specimens of *Austrocochlea concamerata* (Wood), *Chiazacmea flammea* (Q. & G.), *Dicathais textilosa* Lamarck, *Littorina unifasciata* Gray, *Nerita atramentosa* Reeve, *Patella peronii* (Blainville), *Hipponyx conicus* (Schumacher), and *Patelloida alticostata* (Angas).

Reptiles

Woody Island

In November 1950 the Australian Geographic Society expedition recorded 3 reptile species in their short visit—the gecko *Phyllodactylus marmoratus*, *Egernia kingii* and *Hemiergis peronii* (this last listed by Glauert (1954) as *Lygosoma quadridigitatum*). Goodsell et al. (1976) listed 5 species: *Phyllurus milii* (as *Gymnodactylus milii*), *Phyllodactylus marmoratus*, *Egernia multiscutata*, *Ctenotus labillardieri* and *Hemiergis peronii*. However, no specimens were collected, and Dr. G. M. Storr informs us that *E. multiscutata* is probably an error.

Abbott's 2 weeks on Woody I. yielded only 2 lizard species: *Ctenotus labillardieri* and *Egernia napoleonis*, both of which are common. Goodsell et al.'s (1976) record of *E. multiscutata* is probably an error for *E. napoleonis*. Presumably the Australian Geographic Society record of *E. kingii* is also an error for this *Egernia*.

Snakes are definitely absent from Woody I.

Table 4

Mollusc species collected on Mondrain Island in February 1976 which were not collected in November 1950

Family	Species
Chitonidae	* <i>Clavarizona hirtosa</i> (Blainville)
Haliotidae	<i>Haliotus laevigata</i> Donovan <i>H. cornicopora</i> Péron † <i>H. cyclobates</i> Péron
Fissurellidae	† <i>Fissurella nigrita</i> Sowerby
Patellidae	* <i>Patellana iaticostata</i> (Blainville)
Acmaeidae	†* <i>Patelloida nigrosulcata</i> Reeve †* <i>Notoacmaea onychitis</i> (Menke) †* <i>N. septiformis</i> (Quoy & Gaimard)
Trochidae	<i>Phasianotrochus bellulus</i> Dunker <i>Cantharidus lehmanni</i> Menke <i>C. pulcherrima</i> Wood
Phasianellidae	† <i>Tricholia gabiniana</i> Cotton & Godfrey † <i>Orthromesius angasi</i> (Crosse)
Hipponicidae	† <i>Antisabia foliacea</i> (Quoy & Gaimard)
Cypraeidae	† <i>Cypraea piperita</i> Gray † <i>C. comptoni</i> Gray
Cassidae	† <i>Cassis fimbriata</i> (Quoy & Gaimard)
Cymatiidae	† <i>Charonia lampas rubicunda</i> Perry † <i>Cymatiella lesucuri</i> Iredale
Columbellidae	† <i>Macrozafra cominelliformis</i> Tate † <i>Dentimitrella lincolnensis</i> Reeve † <i>D. pulla</i> Gaskin
Mitridae	† <i>Mitra deshayesi</i> d'Orbigny & Recluz
Conidae	† <i>Conus cocceus</i> Reeve
Siphonariidae	†* <i>Siphonaria baconi</i> (Reeve)
Lymnaeidae	† <i>Lymnaea lessona</i> Deshayes
Bulimulidae	<i>Bothriembryon rhodostomus</i> Gray

* living specimens; all others drift shells.

† new record for Archipelago.

Mondrain Island

Two species of snakes and 9 lizard species were found on Mondrain I. (Table 5). Although the Death Adder (*Acanthophis antarcticus*) was recorded in November 1950, it was not met with in February or April. The white-lipped snake *Denisonia coronoides*, apparently collected in 1921, was not recollected in 1950 or 1976 and may be an error. Carpet snakes ranged from 120-175 cm in length, and were usually found on rock, from within a few metres of the sea up into the heath-covered plateau. Crowned snakes (length 25-50 cm) were noted mainly on leaf litter.

Table 5

Counts of Reptiles seen during 10 sunny days at Mondrain Island in February 1976

Species	No. seen
Snakes <i>Python spiloius</i> , Carpet Snake	6
* <i>Denisonia coronata</i> , Crowned Snake	15
Lizards * <i>Amphibolurus ornatus</i>	adult 134
	juv. 71
†* <i>A. muricatus</i>	adult 9
	juv. 6
* <i>Tiliqua rugosa</i> , Bobtail	4
* <i>Ctenotus labillardieri</i>	32
†* <i>Cryptoblepharus virgatus clarus</i>	4
†* <i>Leiolopisma trilineatum</i>	1
<i>Egernia kingii</i>	23
* <i>Phyllodactylus marmoratus</i>	1
<i>Phyllurus milii</i>	1

†new record for the Archipelago.

*Collected, lodged in Western Australian Museum.

The Australian Geographic Society expedition found 8 lizard species. Three of these, *Egernia napoleonis* (as *E. carinata*), *Hermiergus peronii* (as *Lygosoma quadridigitatum*) and *Lerista frosti* (as *Ablepharus elegans*) were not recorded by us. However, we recorded 3 species not only new to the island but also new to the Archipelago (Table 5). The two *Amphibolurus* species lived in different habitats with only slight overlap—*A. ornatus* on rock slabs throughout the island and *A. muricatus* on leaf litter under vegetation and up branches. *Ctenotus labillardieri* was found in leaf litter, under rocks and on rock slabs. King's skink was found mainly close to the shore. We did not find any amphibia on Mondrain I. (where one species was recorded in 1921), even though we specifically searched many rock pools near the summit.

There was insufficient time to attempt a complete search for reptiles on Wilson and Salisbury Is. However, no snakes were observed on either island.

Birds

Mist-netting was carried out on Woody and Mondrain Is. in February 1976. The quantitative estimates of abundance of the bird species trapped are shown in Table 6. The following list records bird species present but not netted on both these islands, and all species noted on Wilson and Salisbury Is. New island records of species are indicated. Seabirds on Woody and Mondrain Is. are more fully described, with maps of their distribution, by Abbott (in press).

Table 6

Relative abundance of mist-netted bird species on two Recherche islands and one adjacent mainland locality

Species	Woody Island		Mondrain Island		East End of Esperance Bay			
	N	RA	N	RA	dune scrub*		heath	
	N	RA	N	RA	N	RA	N	RA
Brown Quail	14	3.7	+	+	—	—	—	—
Brush Bronzewing	1	0.3	—	—	—	—	—	—
Rock Parrot	9	2.4	+	+	+	+	—	—
Velvet Swallow	7	1.8	16	4.9	+	+	2	4.7
Spotted Scrub-Wren	—	—	4	1.2	2	3.2	1	2.3
Golden Whistler	4	1.0	3	0.9	—	—	—	—
Spotted Pardalote	+	+	—	—	1	1.6	1	2.3
Silvereye	67	17.5	36	11.0	51	82.3	49	114.0
Singing Honeyeater	9	2.4	4	1.2	—	—	—	—
White-bearded Honeyeater	59	15.5	93	28.4	1	1.6	54	125.6
Pinebill	—	—	—	—	—	—	3	7.0
Brown Honeyeater	—	—	—	—	—	—	1	2.3
Grey Butcher bird	—	—	—	—	—	—	1	2.3
Total No. net hours	382		327		62		43	
Netting dates	4-14/2/1976		17-26/2/1976		19-24/10/1976			

1 No. trapped of each species

A Relative number of birds trapped (per 100 hr. of netting)

- present but not netted

- absent

this habitat is not represented on Woody and Mondrain Is.

Eudyptula minor Little Penguin.—Woody I., not seen but presence indicated in one place by characteristic guano; Mondrain I., about 5-10 birds braying near camp site, both visits. Feathers were noted at various places along the north coast in April 1977; Salisbury I., one carcass found, and moult feathers elsewhere, amongst limestone boulders at shore (new record).

Turnix ypsilophora Brown Quail.—Woody I., very common, especially in *Avena* paddock. Even more birds were netted than recorded in Table 6 as this species can extricate itself from mist nets; Mondrain I., rare; seen everyday but patchily distributed. Tunney's record of *Turnix varia* on Mondrain (Serventy 1952) may refer to this species.

Phaps elegans Brush Bronzewing.—Woody I., seen everyday. Rare in heath, commonest near *Avena* paddock; Wilson I., two seen.

Pelagodroma marina White-faced Storm-Petrel.—Woody I., burrows found on southeast coast; Mondrain I., a few burrows on south side of peninsula on west coast.

Phalacrocorax fuscescens Black-faced Cormorant.—Woody I., 2-5 usually loafing on rock near extreme east tip of island; Mondrain I., one near landing place and one on rock, 3 m high, near peninsula on west coast.

Hydroprogne caspia Caspian Tern.—Woody I., one offshore, north coast, most days; Mondrain I., one offshore, north coast, February only.

Sterna bergii Crested Tern.—Mondrain I., 14 on north-central point in February; one at same place, April and one near peninsula on west coast.

Larus novaehollandiae Silver Gull.—Woody I., up to 4 present; Mondrain I., 4 at north-central point in April; Wilson I., 20 birds around island.

L. pacificus Pacific Gull.—Woody I., 2-4 seen most days; Mondrain I., one with 2 immatures in February; in April a few around island. On the north coast of this island we counted the number of shells at recently used Pacific Gull anvils where these birds apparently dropped shells of the molluscs *Turbo torquata* and *Dicathais textilis* frequently and of *Haliotis roei* and *Patellanax laticostata* rarely. In order to assess whether these gulls were selecting particular gastropods as prey, we counted shells of gastropods stranded above the high tide in areas of shell rubble and sand along the same stretch of shore as the anvil sites. However, the abundance of such dead remains may not be directly related to the numbers of living animals because of differences between species in mortality rates and shell disintegration rates. Nevertheless, the relative abundances of the stranded shells matched well with Black's impressions of abundances of living gastropods in the adjacent intertidal zone, where *P. laticostata* was very abundant. (In particular two samples of area 10.4 m² and 11 m² had densities of 8.9 and 9.0 individuals/m².)

The results (Table 7) clearly show that Pacific Gulls selected *Turbo* and *Dicathais*. *Haliotis* and *Patellanax* always cling tightly to the rock and increase their grip when disturbed. On the other hand *Turbo* and *Dicathais* withdraw into their shells when disturbed and could therefore be carried off easily. We did not observe any gulls actually capturing gastropods or dropping items on the anvil sites. Wilson I., 4 immatures and 2 adults seen. Salisbury I., a few offshore at landing place.

Haematopus fuliginosus Sooty Oystercatcher.—Woody I., 3 around island; Mondrain I., 5 seen along north shore; Wilson I., one bird on south side; Salisbury I., 2 near landing.

Table 7

Gastropod remains at 14 Pacific Gull anvils on granite shores, and at 8 areas of strand-line drift, on Mondrain Island. February 1976

	<i>Haliotus roei</i>	<i>Patellanax laticostata</i>	<i>Turbo torquata</i>	<i>T. jourdani</i> *	<i>Campanile symbolica</i> *	<i>Dicathais textilosa</i>
Gull anvil	3	4	97	0	0	75
Strand-line drift	27	289	35	4	1	19

 χ^2 test for independence (omitting*) = 333

Tringa hypoleucos Common sandpiper.—Mondrain I., one at north-central point, February (new record for island).

Ardea novaehollandiae White-faced heron.—Mondrain I., one bird at north-central point, February.

Cereopsis novaehollandiae Cape Barren Goose.—Woody I., one pair, observed feeding in *Avena* paddock and on north shore; Mondrain I., always one pair on north shore, and 5 seen at south end; Wilson I., 4 seen together on north side, and another 3 on south side.

Accipiter fasciatus Brown Goshawk.—Woody I., 2 birds (one an immature male) in *E. platypus* forest. One bird killed and ate a rock parrot in mistnet.

Haliaeetus leucogaster White-breasted sea eagle.—Woody I., one overhead on 9 February; Mondrain I., one in April, and one adult and one immature in February; Wilson I., 2 pairs seen. No nests were located on these islands.

Falco peregrinus Peregrine Falcon.—Mondrain I., one bird, glimpsed briefly in centre of island on 26 February, may have been of this species.

F. cenchroides Kestrel.—Mondrain I., one at northwest end in February.

Tyto alba Barn Owl.—Woody I., one bird was seen at 4 a.m. in the *Avena* paddock on 16 February.

Neophema petrophila Rock Parrot.—Woody I., common about *Avena* paddock, where feeding on *Lycium* berries; Mondrain I., feeding amongst *Rhagodia* bushes; Wilson I., heard only.

Cacomantis pyrrhophanus Fan-tailed Cuckoo.—Mondrain I., two birds seen near camp in April (new record for Archipelago).

Hirundo neoxena Welcome Swallow.—Woody I., nests found in caves; about 30 birds seen overhead at dusk several days; Mondrain I., common; Wilson I., a few.

H. nigricans Tree Martin.—Woody I., 12 birds over *Avena* paddock on 15 February.

Coracina novaehollandiae Black-faced Cuckoo-Shrike.—Woody I., one bird seen 11 February; Mondrain I., 2 birds seen northwest end in *Eucalyptus* forest in February. (New record for Archipelago.)

Pachycephala pectoralis Golden Whistler.—Woody I., in *E. platypus* forest only; Mondrain I., in thickets of no great height; Wilson I., one brown-plumaged bird in *Melaleuca globifera* stand, probably vagrant.

Sericornis maculatus Spotted Scrub-wren.—Mondrain I., widespread; Salisbury I., in heath on plateau as well as thinly vegetated slopes down to landing place.

Zosterops lateralis Silvereye.—Woody I., feeding on *Lycium* berries and *Muehlenbeckia* fruits, as well as nectar from *E. platypus* flowers; Mondrain I., feeding on nectar from *M. lanceolata* flowers; Wilson I., only two seen; Salisbury I., rare.

Meliphaga virescens Singing Honeyeater.—Woody I., feeding on *Lycium* berries; Mondrain I., feeding on *M. lanceolata* flowers; Wilson I., a few present.

Phylidonyris novaehollandiae White-bearded Honeyeater.—Woody I., common in *E. platypus* forest, where feeding on nectar; also feeding at *M. elliptica* and *M. lanceolata* flowers. Only one bird seen in open-heath; Mondrain I., feeding from *M. lanceolata* flowers and *E. lehmannii* flowers.

Pardalotus punctatus Spotted Pardalote.—Woody I., one pair seen over several days in *E. platypus* forest; possibly vagrant (New record for Archipelago).

Anthus novaeseelandiae Pipit.—Wilson I., one bird seen.

Corvus coronoides Raven.—Woody I., usually 2-3 recorded, but 15 was most recorded at one time; Mondrain I., 2 seen each day; Wilson I., 2 present.

The quantitative estimates of abundance of 'catchable' birds (Table 6) show that the Silvereye and White-bearded Honeyeater were the most abundant species on Woody and Mondrain Is. and in the heath at the east end of Esperance Bay (*Calothamnus quadrifidus* and *Melaleuca globifera* dominant). The other mainland habitat studied was on Quaternary sand dunes behind the beach, a habitat not represented on Woody or Mondrain Is.

Mammals

Two *Rattus* species (one introduced), 2 macropod species (one introduced) and 2 species of seals were recorded. No trapping was carried out.

Woody Island

Rattus rattus.—This species was abundant at the campsite (edge of *Avena* paddock). At night, scores were seen in this paddock, where they fed on *Avena* seeds and table scraps. They were

ery bold. *R. rattus* has apparently replaced *R. fuscipes* on Woody I., as the latter species as collected there in 1921 (Taylor and Horner 1973).

Macropus fuliginosus.—Probably introduced. A skull was picked up on the shore north of the vena paddock (lodged in the Western Australian Museum); a joey was seen several times in this paddock, and occasionally another larger animal was disturbed at various places in the eastern half of the island.

No seals occur around this island. Goodsell *et al.* (1976), who ran various trap lines, recorded *Pseudomys albocinereus* on Woody I.

Mondrain Island

Rattus fuscipes.—Very rare. Only 2 individuals were seen, both near campsite. One of these drowned in a bucket of water and is lodged in the collections of the Western Australian Museum. Our table scraps were ignored.

Petrogale lateralis Rock wallaby.—These were conspicuous and 67 were counted over our 10 sunny days on the island in February (Table 8). We saw animals at all times of the day. Most of our sightings were along the sloping granite shore and the adjacent piles of boulders which provided refuges for the animals (Table 8). The group of 7 animals was amongst boulders along the shore where there was a seep of freshwater where vegetation met the rock. However, we saw animals far from the shore near the central part of the island on granite outcrops and amongst boulders there. Faeces were seen about the summit. The central heath habitat was the only location in which we failed to see Rock wallabies or find their remains. Many skulls were collected, and have been lodged in the Western Australian Museum. In April 1977, Rock wallabies seemed to be less conspicuous than in February 1976 (Table 9).

In February, close to the shore, Rock wallabies were observed chewing the succulents *Disphyma aucklandii* and *Carpobrotus virescens*, and *Atriplex nerea* at the extreme north western point. In April, *Carpobrotus* was found freshly chewed, and *Myoporum adscendens* was strip-barked.

Neophoca cinerea Australian Sea Lion.—These were seen, in February, occasionally in the water at the landing place, and on the tip of the north central point (2 animals). A skull and old faeces were found about half way down the east side of the island close to the shore. In April, 4 were on the same north central point, and one appeared briefly at the landing place but did not land. No individuals or old faeces were found amongst the vegetation of the island. This is a common trait of this species.

Arctocephalus forsteri New Zealand fur seal.—One on north central point in February, and 2 were seen close to this point on a boulder islet in April.

Wilson Island

Petrogale lateralis.—The most abundant (and conspicuous) population in the Recherche islands visited was found on Wilson I. (Table 9). Plant species eaten were *Poa australis* tussocks, *Carpobrotus virescens*, *Lomandra rigida* and *Myoporum adscendens* (bark).

No seals, or their old faeces, were found.

Salisbury Island

Petrogale lateralis.—Because this island is the third largest in the Archipelago, and because so little time was spent there, any count of wallabies is probably worthless (Table 9). However, in qualitative terms, the population here was intermediate in abundance between those of Mondrain and Wilson Is. in April 1977. The leaves of *Poa australis* and *Olcara axillaris* were found chewed, and *Myoporum adscendens* was ring-barked.

Arctocephalus forsteri.—Nine, including one pup, were seen on the granite platform near the landing. There are many large caves at the base of the island (formed by nick points in limestone, and the openings are usually protected by debris). Dr. G. Maynes reported about 20 more seals farther south of the landing.

Discussion

Biogeographical considerations

No plant, mollusc, reptile, bird or mammal species is known to be restricted to any of the Recherche islands—species either occur on the mainland or on other islands along southern Australia. However, the archipelago provides a largely neglected 'natural laboratory' (Main 1967) in which to carry out ecological, evolutionary, morphological and genetic studies. Very importantly, much of the mainland opposite the Archipelago is reserved as National Park, so that mainland/island comparisons of ecological/evolutionary interest are still possible. This desirable feature is becoming less available elsewhere in southwest Australia. A variety of animals occurs abundantly on enough islands and on the mainland to make such studies feasible (e.g. *Amphibolurus ornatus*, Crowned snake, two macropod species).

Several species of reptiles and mammals which are now extinct on the adjacent mainland still occur on some of the islands. Three of the lizard species collected by us on Mondrain I.

Table 8

Sightings of 67 Rock Wallabies during 10 sunny days at Mondrain Island in February 1976

	Vegetation	Granite Outcrops	Boulders in vegetation	Boulders at shore	Rock at shore
o. single individuals	7	5	3	15	6
o. individuals in groups	0	0	2,2,3	2,2,2,3,5,7,	3

Table 9
Numbers of Rock Wallabies seen on three Recherche Islands

Island	No. seen	Period of observation	Island area (ha)
Mondrain	67	10 sunny days, February 1976	787
Mondrain	7	2 days, April 1977	787
Wilson	37	4 hours, 25 April 1977	123
Salisbury	5	1.5 hours, 28 April 1977	316

have not been recorded for Cape Le Grand National Park (Chapman and Dell 1975). *Python spiloptus* is rare in this Park but common on Mondrain I. Rock wallabies and Tammars, apparently now extinct in the Park (Kitchener and Chapman in Kitchener *et al.* 1975), are abundant on several islands (Serventy 1953, this study). The Cape Barren Goose, not recorded from the Park, occurs on many islands (Serventy 1952, this study).

The distribution of snakes throughout the Archipelago (Serventy in Glauert 1954) would repay further study. The Carpet snake is known only from Mondrain I., the Dugite only from two islands in the west group of islands, the Crowned Snake from three widely separated islands, with the Death Adder having been definitely observed on five widely separated islands. The largest island in the Archipelago, Middle I., has no snakes. The Tiger Snake, one of the most abundant snakes in Cape Le Grand Park (Chapman and Dell in Kitchener *et al.* 1975) is not known from any Recherche island, and the Death Adder was not recorded from the Park.

Insular distribution of Rock wallabies

Of about 220 above-water land masses in the Archipelago, 20 have an area of 90 ha or more. The smallest island with a macropod population is Combe (area 93 ha). Only another 5 islands have macropod populations. The interesting problem of why the remaining 14 islands do not have either the Rock wallaby or Tammar has not been addressed before. All of these appear to be large enough to support the Rock wallaby, which is smaller than the Tammar so that more reproductive units would be available. Main (1961) and Main and Yadav (1971) suggest that indestructible rock-piles allow Rock wallabies to persist on an island as small as Combe. However, Abbott has sailed close-in down the west shore of Combe, and in his opinion, the island does not appear to have any more rock piles than, for example, Woody I. It may be useful to examine more closely the floras of the 4 islands possessing Rock wallabies to see whether plant species preferred by Rock wallabies are rare or absent from the 16 islands without Rock wallabies.

Our observations suggest that the succulents *Disphyma*, *Carpobrotus* and *Atriplex* with *Poa* tussocks and the common *Olearia* and *Myoporum* are important elements in the diet of Rock wallabies. An island with a flora and vegetation made up entirely of these species should therefore have a better chance of keeping

a viable Rock wallaby population than an island covered with heath or *Eucalyptus* forest (such as Woody I. or Sandy Hook I.). Also considerations of wave action suggest that islands more offshore should develop a more halophytic flora and vegetation than inshore islands because most sclerophyllous species do not persist under exposed maritime conditions (Abbott, unpublished). This may help to explain why Rock wallabies are on the older islands (Table 10) in the Archipelago (Salisbury, Wilson, Combe and Mondrain) and not on the younger ones (e.g. Middle, North Twin Peaks, Woody, Observatory Is.).

Some of the islands listed in Table 10 should prove suitable sites on which to liberate Rock wallabies. Introduction in 1960 of one male, 4 females and one unsexed individual of the Rock wallaby to the Middle and South Pearson Islands from North Pearson I. (South Australia) led to a population of 90-112 animals by 1969 (Thomas and Delroy 1971).

Turnover.

Studies of turnover (the frequency with which species become extinct, or immigrate) are becoming popular (Diamond 1969; Lynch and Johnson 1974; Abbott 1977). Such studies have value only if surveys are thorough and complete, and obviously the reliability of turnover studies depends on the taxon considered and the size of the island. If islands are too large, species will be overlooked (and mistakenly assumed to have become extinct), or be regarded as immigrants when they have been present all the time. Islands such as the 4 studied in this paper seem to be too large to make estimates of turnover of plant or reptile species reliable enough. However, such studies with land bird and mammal species are entirely appropriate.

As the Australian Geographic Society expedition spent only some 2 hours on Woody I., we do not have a sufficient baseline of the birds present in 1950. However, we can compare Goodsell *et al.*'s (1976) list (October-November 1975) with Abbott's visit of February 1976. Goodsell *et al.* recorded 14 land bird species of which 2 (Swamp Harrier and Kestrel) were represented by single individuals. Abbott recorded 15 species. Three of these (Tree Martin, Spotted Pardalote and Black-faced Cuckoo-shrike) were new and were probably vagrant, except possibly the Spotted Pardalote.

On Mondrain I., Serventy (1952) recorded 8 species of land birds. We recorded 13 species of which the Brown Quail, Cape Barren Goose, Kestrel, Fan-tailed Cuckoo (April only), and

Table 10

Area, elevation and age (as indicated by depth of surrounding water) of Recherche islands apparently large enough to support a species of Macropod

Island	Area (ha)	Elevation (m)	Rising from Sea (m)**
†Middle	1 110	175	33
*Mondrain	787	226	45
*Salisbury	316	119	82
†North Twin Peak	306	187	18
Figure of 8	273	113	45
Sandy Hook	268	140	c.35
Boxer	192	88	42
Woody	188	130	36
Long	152	103	c.29
*Wilson	123	80	c.49
Remark	116	220	c.29
South Twin Peak	115	186	c.27
Frederick	106	88	c.29
Hood	106	76	c.45
Corbett	99	124	c.50
Observatory	96	78	29
Gunton	94	116	40
Charley	93	108	24
*Combe	93	22	60
Howe	90	82	c.45

* Rock Wallaby present. These islands are also some of the oldest in the Archipelago.

† Tammar present

** A depth of e.g. 82 m signifies that island formed about 15 000 yr. B.P. (Main 1961). Sea level continued to rise at the rate of c. 1 m per century.

Black-faced Cuckoo-shrike (February only) were new. The first 2 probably breed on the island.

Serventy (1952) recorded 4 land bird species on Salisbury I. in November 1950 whereas Abbott recorded only 2 in April 1977, but in view of the shortness of these visits, these differences mean little. For the mammals, the same 2 species of land mammals were recorded on Mondrain I. in 1921 and 1976. On Salisbury I., the Rock wallaby and New Zealand Fur Seal were recorded in 1950 and 1977.

Thus the breeding bird and mammal faunas show remarkable stability over time.

Relevance to design of reserves on mainland

It is no surprise that small, circumscribed areas have fewer species than areas of equal size that are part of a larger area. The majority of species in a community are the rare ones (Preston 1962; Williams 1964), and in a mainland situation disappearance of these rare species from a small area can usually be made good by dispersing individuals. This process of recolonization on islands is attenuated by a stretch of water—a bird species that stops to rest will drown, a fruit or seed of many plant species will sink or if it reaches an island, may not germinate.

Certain bird species (e.g. Hawk, Raven, White-bearded Honeyeater, Silvereye, Rock parrot, Swallow, Spotted pardalote, Black-faced Cuckoo-shrike, Cuckoos) are capable of sustained flight and these species are present on or have been recorded on some of the Recherche islands. Other bird species (Golden Whistler, Scrub-wren, Singing Honeyeater) are not known to make extensive movements on the mainland, and so it seems probable that these species were originally on the Recherche islands when they were hills on the mainland, and have survived on some islands to the present day.

The Recherche islands and the adjacent mainland present a situation that is little faced by authorities today but which will become critical over the next 100 years in Western Australia. This is, given that clearing for agriculture will continue, is it better to retain a few large tracts of native habitat or the equivalent area in many, smaller reserves? (Wilson and Willis 1975; Simberloff and Abele 1976.) Both seem to be required. The latter alternative by itself does not guarantee the persistence of high diversity communities because of high extinction rates of species in small areas. However, the former leads to reserves with many species of which only a few are abundant. Furthermore in an Archipelago, species (e.g. Rock wallabies, various snakes) that would otherwise become rare in larger areas can persist, perhaps because of reduced interspecific competition, or predation.

Acknowledgments.—Our visits to the islands in February 1976 were financed by an Australian Research Grants Committee grant to I. Abbott. The visit in April 1977 was made possible by Dr. G. M. Maynes, Macquarie University, N.S.W. Permission to work on the islands was given by the Western Australian Wild Life Authority. We are very grateful to the following for assistance: Dr. F. Wells (identification of molluscs), Dr. J. H. Willis, Mr. A. S. George, Mr. B. R. Maslin, and Mr. P. G. Wilson (identification of plant species); Dr. G. M. Storr and Mr. L. Smith (identification of reptiles); Dr. J. W. Green (access to R. D. Royce's field notebooks); Mr. A. Miller (loan of aerial mosaics from which island areas were calculated). We thank Dr. J. H. Willis for comments on the manuscript.

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